LINNAEUS, THE CORTEX-MEDULLA THEORY, AND THE KEY TO HIS UNDERSTANDING OF PLANT FORM AND NATURAL RELATIONSHIPS

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Linnaeus's ideas on the composition of the various parts of the plant and the generation of plant form by the interactions of these tissues both with each other and with the sap of the plant are outlined. Linnaeus used the analogy he drew between the vegetative plant and the larva of an insect to justify his emphasis on parts of the fructification in the classification of genera; as with insects, he used the adult, rather than the larva, in classification. His thoughts on the relationship between the various appendicular parts of the plant in the context of his theories of prolepsis and metamorphosis are summarized. Linnaeus's ideas of plant form support his theories on the generation of plant diversity by hybridization and are closely connected with his description of plenitude—continuity in a largely macroscopic world of systematically arranged form that also incorporated findings from the microscopic world. Here, as elsewhere, the medulla can be shown to be the seat of life, but only its interaction with cortex allowed stable form to become manifest. Goethe's and A. P. de Candolle's notions of the "metamorphosis" of plants are briefly situated with regard to Linnaeus's ideas, as is the work of some earlier botanists. In the discussion the interrelationship is explored between Linnaeus's different approaches to looking at plants and their significance for an understanding both of his taxonomic work and of his more general thinking about the diversity of life. The ideas of Linnaeus, and especially those of Goethe, on the metamorphosis of plant form are situated at one end of a spectrum of responses to the problem of the comprehension of diversity; Linnaeus's own taxonomic system represents the opposite end. The archaic cast to Linnaeus's cortex-medulla theory is confirmed, although its coherence and explanatory powers are abundantly evident.

Most commentaries on Linnaeus's biological work have focused on his idea that the taxonomically important characters of an organism reflect, or are, that organism's essence, and especially on his arrangement of organisms in a classification using these characters. Any ideas that Linnaeus may have had as to how the form of an organism becomes manifest, and how the diversity of form in the living work is generated and organized, are less frequently discussed. It is usually suggested (see, for example, Stearn, 1957, and Gustafsson, 1985) that Linnaeus was perhaps more interested in simply describing the world than in understanding laws or principles underlying the diversity of form present in

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it. However, it is becoming abundantly evident that this is not an accurate perception of his activities, as perusal of the numerous theses written by Linnaeus and defended by his students shows. Largely using these theses, Guédès (1969) outlined the development of Linnaeus's ideas on plant morphology and development; Larson (1971) emphasized the Aristotelian dimensions of Linnaeus's thought and discussed his ideas on plant hybridization in some detail; and Broberg (1985), in a remarkable article, succeeded in pulling together much of the underlying body of theory in these theses and showed clearly the important synthetic component in Linnaeus's writings. One goal of this paper is to bring together these different parts of the story, emphasizing its botanical dimension in particular. We also hope to deepen the appreciation of Linnaeus's important efforts to develop an understanding of organic form and diversity, at the same time stressing the relationship of his thought to that of his immediate predecessors and successors.

Larson (1971) clearly outlined what is, as he noted, largely implicit in the work that embodies Linnaeus's taxonomic principles, the *Philosophia Botanica* (Linnaeus, 1751a): all genera are natural—the work of nature—and form the foundation of theoretical botany. Such genera were to be recognized by distinctive and constant features in the various parts of the fructification, these being the most essential parts of the plant. To quote Larson (1971, p. 93): "The 'naturalness' of Linnaean genera rests, then, upon assumptions about the principles of activity for the performance of which plants have come into being. The nature of the genus has a narrower sense than 'reality': it is the formative factor in reality."

Cain (1958, pp. 154, 155, quoting Maritain, 1983) suggested that "nature" or "essence," although originally in Aristotelian thought referring to those principles of the activity for which an organism came into being—the final cause—might also be restricted simply to "what a thing is," its visible characters. To quote Larson (1971, p. 93) again, "The simple elements of the fructification, when isolated, and given explicit form, teach the naturalist the characters of the genera spelled out by the hand of God." But between God (a cosmic final cause) and explicit form (formal cause), there are other levels of causality. There is the organism with its role in the community (see, for example, Linnaeus, 1749, 1760b),[3] a local final cause. There are also the material and efficient causes of explicit form, which cause any particular form to be what it is, and it is with these levels of understanding of form in Linnaeus's botanical thought that we are mainly concerned here. Although the focus of this paper is not Aristotelian causality in Linnaean thought, it should be remembered that Linnaeus's biological thought as a whole has a decidedly Aristotelian background (Larson, 1971).

This leads to an underemphasized aspect of Linnaeus's work that he developed most actively after about 1749. He suggested that the "formative factor"

[3]Following authors such as Stearn (1966), authorship of the Linnaean theses is to be ascribed to Linnaeus himself, not to the defendant whose name is on the title page. One of the very few cases where the actual defender of the thesis had some hand in its writing is the important *Gemmae Arborum* (see also below). This thesis alone is cited under its defender, Löfling.

of a plant is the medulla: without the medulla, or when the medulla is depleted, the plant dies; through the medulla, the unchanging essence of the plant is transmitted through successive generations. Interaction of the medulla with the cortex leads to the development of all the parts of the plant from cotyledons to pistils; in the flower, in particular, the medulla interacts successively with the different tissues derived from the cortex, each interaction producing a different part of the flower. Although all these parts other than the pistil come entirely from the cortex, the pistil being largely medulla, they cannot develop without the stimulation of the medulla. The parts of the fructification, which include the flower, are of course the basis of most Linnaean genera.

Ideas such as these are discussed at length in a series of theses, especially *Gemmae Arborum* (Löfling, 1749), *Metamorphoses Plantarum* (Linnaeus, 1755a), *Prolepsis Plantarum* (1760c, 1763), *Fundamentum Fructificationis* (1762b), and *Mundum Invisibilem* (1767a). These theses are often extended justifications for positions Linnaeus only outlined in better-known works such as the *Philosophia Botanica* (1751a) and the tenth and subsequent editions of the *Systema Naturae* (e.g., 1759b, 1767b). They owe much to classic notions of the plant body, in particular those of Cesalpino, whom Linnaeus frequently acknowledged, and through Cesalpino, Theophrastus and Aristotle. They are also intimately linked with complex analyses of the relationships between plant parts, which are little connected with Linnaeus's use of plant structure in his systematic studies.

In these more purely morphological analyses, Linnaeus suggested that there was a fundamental similarity (and often interchangeability) between cotyledons, leaves, sepals, stamens, and the like—in fact, between all the appendicular parts of the plant (this term is used without any implication as to what these structures "really" are) except the carpels, and that exception, as we shall see, holds only in some respects. The observations that Linnaeus emphasized in establishing these similarities were very different from those he used in grouping species to form genera, and genera to form families or ordines naturales, as in the fragments of his natural system. He focused on nonessential variation, adopted what might be called a physiological-balance theory of plant reproduction and morphogenesis, and emphasized a parallel between vegetative and floral buds, and, more generally, a whole variety of "budlike" structures in the plant, including the embryo in the seed. Both his systematic and his morphological studies led to an emphasis on continuity of form, but the forms emphasized were different.[4]

Focusing on these aspects of Linnaeus's thought allows us to understand his later work more clearly and perhaps puts his so-called failure or inability to develop more than the bare outlines of a natural system, the development of which he clearly considered to be very desirable, in a somewhat different light. In addition to classifying all the new material that was being sent to him,

[4]Johann Wolfgang Goethe and Augustin-Pyramus de Candolle are usually considered two of the most important early proponents of ideas concerning the fundamental similarity of all plant parts, although the former had little immediate influence in systematic botany (see Guédès, 1969; Cusset, 1982). C. F. Wolff outlined similar ideas in 1766 (Mueller, 1952).

Linnaeus was developing ideas very different from those we commonly attribute to him. Gustafsson (1985, p. 126) noted, "For Linnaeus the crucial aspect of his work (and the only way in which he could, under the assumptions and axioms of his time, proceed) consisted in observing differences in nature at the cost of the similarities. That is, he stressed the *hierarchic* aspect and was forced to ignore *continuity*." He went on to discuss the attempt to depict the chain of being as a specially constructed analytical language. Even if, following Gustafsson, such an attempt is deemed in principle impossible, we see Linnaeus effectively dealing with continuity in his *morphological* work, and he of course adumbrated the problem of continuity in the context of his natural system (e.g., Linnaeus, 1751a; see especially Broberg, 1985). Between Linnaeus's more or less analytical system and his belief that God's handiwork was visible in the natural world lies a complex and incomplete set of theory and observation that explains at an intermediate level organic form in the botanical world. It is centered on the ancient idea that the plant body is made up of cortex and medulla, and it emphasizes continuity. Here Linnaeus's "passion for synthesis" (Broberg, 1985, p. 179) finds its full expression.

Below we outline the different aspects of this "passion for synthesis," treating each more or less separately. These aspects are cross-referenced to indicate the interrelationship of the several strands of Linnaeus's thought that together form a skein of considerable intricacy.

THE CORTEX-MEDULLA THEORY OF PLANT CONSTRUCTION

Introduction

The cortex-medulla theory of plant construction, in which all parts of the plant are equated with tissues derived from the cortex, or with medullary tissue, first figured prominently in Linnaeus's work in the thesis *Gemmae Arborum*, defended by Pehr Löfling in 1749. Although mentioned in earlier works, it was there always in a much less central position. Löfling's thesis coupled the classical conception of the flower in which the outer, vegetative cortex splits to reveal the inner tissues of the plant with an extensive, but sketchy, elaboration of the cortex-medulla theory. Löfling drew an analogy between the vegetative parts of the plant and the larva of an insect; he looked at budlike structures in general and considered them to be directly comparable; and he examined in some detail the growth of floral and vegetative parts of the plant, entertaining the notion that at least some flowers were precociously developed shoots. This leads to the idea that the parts of the plant other than the stem and root (i.e., all the major organs borne on the shoot) are fundamentally equivalent.

It is interesting to note that this thesis is one of the very few in which the student defending it is supposed to have had an appreciable part in its writing.[5]

[5]This student, Pehr Löfling (1729–1756), also helped to write the *Philosophia Botanica* (Linnaeus, 1751a) at Linnaeus's dictation, Linnaeus being unwell at the time. There are further developments in the ideas mentioned above in this book. During dictation, Löfling questioned things he could not understand, so becoming throughly grounded in Linnaean botany (Blunt, 1971; see Löfling, 1758, p. [3] of the *Företal* written by Linnaeus). One of Linnaeus's best and favorite students, Löfling unfortunately died young while collecting in South America.

PROBLEMA BOTANICUM

in gratiam D:NI AUCTORIS propositum

A

PRÆSIDE.

I. Corpus VEGETABILE constat *Medulla*, vestita *Ligno*, facto ex *Libero*, postquam secessit ab interiori substantia *Corticis*, qui ipse *Epidermide* induitur.

2. *Medulla* cum tegumentis crescit sese in longitudinem præprimis extendendo, fibrasque in latitudinem versus Folia protrudendo.

3. Fibræ medullaris extremitas per corticem protrusa, solvitur sæpius in *Gemmam* ex foliolis imbricatam.

4. *Folium* expanditur attrahendo succum nutritium, quem modicum gemmæ concedit, antequam cadit, nunquam renasciturum.

5. *Gemma* (3) compendium futuræ herbæ extenditur in ramum; hic in ramulos, inque infinitum, donec fructificatio imponat ultimum terminum antiquæ vegetationi.

6. *Calyx* fit intra gemmam ex foliis non secedentibus, deficiente vi eadem removente expandenteque; probant hoc *Nigellæ*, *Rosa*, *Diapensia*, *Perianthium commune*, *Involucrum*, & ex *Salicis* amento insectifera *rosa*.

7. Hoc facto rumpitur intra calycem ramuli apex, secundum leges cuique substantiæ (1) proprias, inque *Florem* expanditur annuo spatio præcocius.

8. *Corollam* teneram, magis mollem & caducam oriri ex corticis, nunc Calycis (6), propria substantia, pulposo libero, confirmant *Flores vernales*, præprimis *Daphnes*, eo tempore, quo Liberi substantia a cortice non recessit.

9. *Stamina* fieri ex substantia lignea (1), olim libero, probat *consistentia*, *situs*, *plenitudo* florum e vegetatione vegetiori, ubi ex molli libero indurescere lignum non permisit tortior propulsio.

10. *Pistillum* centri floris, ex propria eaque medullari substantia ortum est, cum alia hoc in loco supersit nulla.

11. *Fructus* ex pistillo medullari nequit vitam novæ plantæ inchoare, nisi prius staminum essentia lignea absorpta fuerit ab humore medullari pistilli.

12. Quæ itaque caussa connexionis foliorum in Calycem? quo ramuli apex præcocius rumpatur in florem? *Quæ vis mirabilis hujus effectus?* Nodum extremum vegetationis videtur mihi solvisse, qui hunc explicet Gordium.

FIGURE 1. Linnaeus's questions in the thesis *Gemmae Arborum* (Löfling, 1749, facing p. [i]).

There is, however, a further complication that makes the authorship of the ideas in this thesis uncertain. Facing the first page is a series of 11 aphoristic statements concerning plant construction and development and a final series of questions addressing the forces involved in the phenomenon of flowering. This page, headed "Problems in botany proposed to the glory of God by the president [Linnaeus] of the author [Löfling]," is placed at the end of the reprinted versions of the thesis (e.g., Linnaeus, 1751b, 1786) and has largely been overlooked (but cf. Stafleu, 1971). A reproduction of this crucial page is given here (see FIGURE 1), and a free translation follows.

1. The VEGETABLE body is composed of the *Medulla*, covered by *Lignum* [wood], made from *Liber* [phloem and cambium], after it separates from the inner substance of the *Cortex*, which itself is overlain by the *Epidermis*.
2. The *Medulla* with coverings grows by itself, extending mainly in length and pushing out fibers to the side toward the leaves.
3. The extremity of the medullary fiber protrudes through the cortex, often being broken up in the imbricate *Bud* [made up] of small leaves.
4. The expanded *Leaf*, attracting nutritive sap, which, before it falls, allows a modicum to the bud, never being borne again.
5. The *Bud* (3), the compendium of the future vegetative plant being extended into a branch, first as a twig, then to infinity, up to the time when the fructification imposes the final termination of the growth of the old plant.
6. The *Calyx* being within the bud, [made up] of leaves that do not separate, lacking the force to separate and expand; *Nigella, Rosa, Diapensia, common Perianth, Involucre,* and *Salicis* amento insectifera *rosa* demonstrate this.
7. In this way the apex of the branch is torn apart within the calyx, the substances (1) [the tissues of the plant] following laws that are proper, I say the *Flower* expanding a year precociously.
8. The thin corolla, very soft and caducous arising from the cortex, now [part] of the Calyx (6), the true substance, fleshy liber, *spring Flowers*, especially *Daphne*, confirm at that time when the substance of the Liber does not separate from the cortex.
9. The *Stamens* being derived from the woody substance (1), once liber, the *existence, position*, the *completeness* of the flowers from more vigorous plant show, where the hardened lignum did not allow stronger propulsion from the soft liber.
10. The *Pistil* of the center of the flower, [made] from its special substance of the medulla, with nothing else remaining in that place.
11. The *Fruit* from the pistil [made up] of the medulla is unable to lay the foundations for the life of the new plant, unless first the woody essence of the stamen is absorbed by the medullary humor of the pistil.
12. What then [is] the cause of the joining of the leaves in the Calyx? by what is the precocious apex of the plant torn apart in the flower?

What miraculous force does this?

It appears to me that the ultimate node of the plant is dissolved, as was loosened the Gordian [knot].

The contents of this introductory page outline many of the points that Linnaeus developed over the next fifteen years. It is interesting, and perhaps relevant in attempts to understand authorship of the various parts of this thesis, to note that the emphasis on those forces in the plant that might account for the morphological phenomena observed is not so evident in the body of Löfling's thesis. This, however, is clearly seen to be the central point at issue, as the emphasis on the final statements, possibly written by Linnaeus himself, suggests.

The Basic Construction and Development of the Plant Body

Linnaeus (e.g., 1751a) consistently divided the plant body into three basic parts: the *radix,* or root; the *herba,* or vegetative region of the plant, sometimes simply called "planta" (e.g., Linnaeus, 1741, p. 12); and the *fructificatio,* everything from the calyx to the seed.[6] The root, which took up food from the soil, produced the vegetative part of the plant as well as the fructification. The plant body as a whole was made up of a central medulla, roughly corresponding to the pith, covered by the lignum (wood). This latter arose from the liber (inner bark: phloem and cambium), which was in turn derived from the cortex, itself overlain by the epidermis (see Table 1). These several tissue types could be reduced to two, the cortex and the medulla (Linnaeus, 1759a, p. 4; the "corporea externa" and the "medulla interna" in Linnaeus, 1767b, p. 7), by emphasizing that the lignum and the liber were both derived from the cortex.

In Linnaeus's taxonomic analyses the fructification was divided into two parts, the flower and the fruit, the former being made up of calyx, corolla, stamens, and pistil, and the latter of pericarp, seed, and receptacle (e.g., Linnaeus, 1751a). Linnaeus had very early integrated some of the organs of the fructification with the cortex-medulla division of plant tissue (see Table 1). He thought that the thicker outer cortex formed the calyx, and the thinner inner cortex, the petals; the stamens came from the wood, and the pistil from the medulla (Linnaeus, 1738; see Figure 2A). Thus the inner parts of the plant were displayed by the splitting of the cortex in the flower (see, for example,

[6]Initially the "planta" was thought of as being composed of the trunk, the leaves, the "fulcra" (stipules, prickles, and the like), and the fructification (Linnaeus, 1736a, p. 7).

Table 1. **The main organ categories of the plant and their origin.**

Main plant parts			Tissue types	
Main categories		**Organs**	**Normal arrangement**	**Linnaeus, 1746†**
Radix	Root	Root	Cortex + medulla	—
Herba (planta)	Vegetative plant	Stem	Cortex + medulla	Cortex + medulla
		Leaf	Cortex	Cortex
		Thorns, etc. ("fulcra")	Presumably cortex	Presumably cortex
Fructificatio	Flower	Calyx*	Cortex	Outer cortex
		Corolla*	Liber	Inner cortex
		Stamens*	Lignum	Alburnum
		Pistil*	Medulla	—
	Fruit	Pericarp*	—	Lignum
		Seed*	Medulla‡	Medulla‡
		Receptacle*	—	—

*The seven parts of the fructification.

†This is closer to Cesalpinian ideas as to the equivalence of organ categories with tissue types, see below.

‡The cortex became involved in the production of the seed via the process of fertilization.

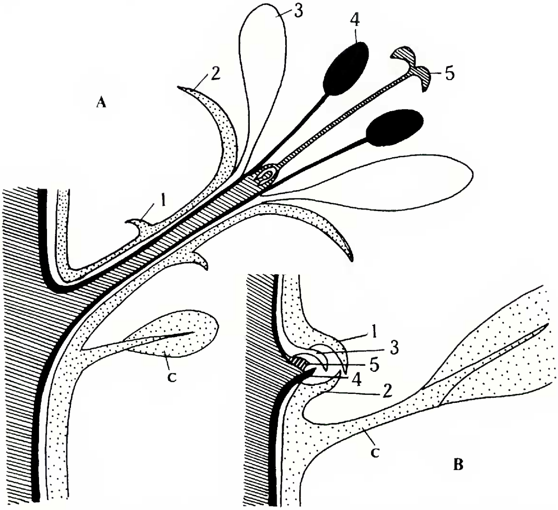

FIGURE 2. Linnaeus's ideas on the construction of the plant body: A, flower; B, vegetative bud (stipple = cortex, black = liber, white = wood, ascending diagonal lines = membranes surrounding medulla, descending diagonal lines = medulla. 1 = first year's growth, 2 = second year's growth, and so on; c = leaf on current year's growth). In flower all growth occurs in a single year (anticipation), in vegetative bud it occurs over several years; for diagrammatic purposes, a single leaf represents each year's growth.

Löfling, 1749, p. 13, footnote s; Linnaeus, e.g., 1755b, p. 5). However, the exact details of this oft-repeated comparison differed. After equating the various organs of the flower with those of the vertebrate reproductive system, Linnaeus (1746) briefly mentioned that the calyx was made up of outer cortex, the corolla from inner cortex, the stamens from nutritive alburnum (sapwood, corresponding to the liber), the pericarp from ligneous substance, and the seed from medulla. Here both parts of the fructification, flower and fruit, derive from the several parts of the basic tissue system of the plant, but usually it was the flower alone that was compared with these tissues (see FIGURE 2A; Löfling, 1749, cf. facing p. [1] and p. 13; Linnaeus, 1751a, 1751c (the medulla produces the seed), 1755a, 1759b). If bracts were included in this comparison, they, too, were considered to be formed from the cortex (Linnaeus, 1763).

In the vegetative plant the ends of the medullary fibers protruded through the cortex, liber, and wood and stimulated the formation of leaves from the cortex (see FIGURE 2B). The young leaves formed imbricate buds with medulla in the center; the buds themselves did not develop from leaves. Thus the vegetative region of the plant was effectively an assemblage of buds, a composite, or—in modern terminology—a modular organism, that could repeat itself *ad infinitum* unless terminated by the fructification (Löfling, 1749) or the death of the medulla. The medulla was both the form-generating part of the plant and the part that ensured the plant's continued growth; all parts of the plant with the potential for growth had medulla.

Linnaeus (1763) expanded this point in the thesis *Prolepsi Plantarum.* Each of the numerous buds on a tree contained medulla, which, growing out and dividing incessantly, continued the life of the plant, the ultimate fibers of the medulla being in the next generation of buds. Thus, only a few years after a willow twig is put in the ground, the subdivision of the medulla in the buds of that original twig results in a large, copiously branched tree from which twigs can be plucked and planted; the whole process can then repeat itself. In an annual plant, on the other hand, Linnaeus thought that there were no buds, only flowers in the axils of the leaves. This meant that the medulla in each axil was used up in the production of the flowers; the plant then died since it had no medulla left (Linnaeus, 1760c). Hence the only difference between annuals and perennials was that in the former the medulla was quickly used up in the fructification, while in the latter it was for the most part retained in the trunk or root and could produce more buds.

Linnaeus's concept of plant growth contained two antagonistic tendencies or movements involved in growth and development. A movement from the outside of the plant that was manifest in the direction of development of the cortex-derived tissues was nutritive and descending, while that from the inside to the outside was ascending and generative: "the life of the medulla, spongy, divisible by multiplication and with an infinity of endings, growing upwards, incarcerated in the Cortical *Body,* which is nutritive, descending, joined to the ground . . ." (Linnaeus, 1759b, pp. 826, 827; there are extended comparisons with animals in several places—e.g., Linnaeus, 1751a, 1759a). The cortex could be compared to the vascular system; the mouth, or ventricle, of the plant was in the ground, from which the roots drew up nourishment that was purified in the leaves. As elsewhere in this theoretical edifice, there are problems in the interpretation: the force in the cortex is descending, but food is taken (ingested) from the ground. In any case these forces do not exactly correspond to other visualizations of the plant: the three main morphological subdivisions of the plant body are root, vegetative plant, and fructification (see TABLE 1).

In the seed, which was the rudiment of the new plant, the plumule was the scaly, ascending part of the corculum (the plumule-radicle junction and, to many classical authors, the "heart" of the plant). When bathed in sap (humore), the bud could grow *ad infinitum.* The rostellum was the simple, descending part (Linnaeus, 1751a). The above-ground plant was produced from the root. Nothing new was formed; instead, there was simple continuity through the medulla ("Nova *creatio* nulla, sed *continuata* generatio, cum *Corculum* seminis constat parte radicis medullari": *ibid.,* p. 38). As will be seen, the balance of the upward and downward forces in the plant affected the *kind* of organs it produced, especially whether they were floral or vegetative. The particular *form* of each organ was a manifestation of the essence of the species, although taxonomically unimportant details were due to accidental causes such as a change in the environment or the growth of galls.

Linnaeus returned to the interaction of these tissues with each other and the growth forces of the plant in numerous works (e.g., Linnaeus, 1759a; 1759b, p. 827, translated below; 1767c):

> the plant with the rootlets sucking the humid envelopment (tincturam aquosam) of the ground, which by the heat [that] is daily added, is pushed through the *cortex,* whence the nutrition of the plant, breathing out the superfluous, deposits *liber* on the inner surface ("pariete"), every year separating as *woody* substance, holding up the ascending stem, within which the multiplying *medulla,* the base dissolving, the apex infinite, although I conceive the bundle of fibers as a growing isosceles [triangle], in which stronger force tears apart the outer fibers, diverging outward and penetrating the cortex, terminating in a bud that multiplies similarly; from the obstacle of the cortex appear the expanded leaf, breathing air, looking at the sun, exercised by the movement of the wind, never to be born again; where in truth the force being less driven, the medullary fibers converge, and in protruding they lay bare the substance of the cortex in the *calyx,* of the liber in the *corolla,* of the wood in the *stamen,* of the medulla in the *pistil,* the plant ending in new life, the collected threads in the *seeds* are the last of the medulla.

Thus the medulla was indeed involved in the generation of all the appendicular organs. The leaves could not reproduce themselves or give rise to buds; when a bud, containing medulla, was removed, leaves would never be produced again (see above, also Linnaeus, 1760b). Leaf, petal, and stamen alike were dependent on medulla for their existence, although their substance was cortical in nature. In a very brief summary of the growth of the plant, Linnaeus (1751a, p. 301) even suggested that the whole vegetative part of the plant above the ground (herba) was the product of the medullary substance of the root.

The Analogy between Larvae of Insects and the Vegetative Organs of Plants

Löfling (1749) described the bud as being the larva of the herb—i.e., of the vegetative part of the plant. Linnaeus quickly developed this analogy. There was a metamorphosis in the plant, like that recorded by Jan Swammerdam in cabbage white butterflies: the caterpillar pupated; later the pupa or chrysalis broke through the cortex and metamorphosed, and the butterfly, the perfect form of the insect, emerged (Linnaeus, 1749). Note that this and other analogies Linnaeus used go far beyond mere comparability; they betoken more what we would think of as homologies (Stevens, 1984a, 1984b; Broberg, 1985; see especially Beer, 1983, chapter 3, and Atran, 1990, including references).

> And so it is and will be true, that whoever wishes to understand plants correctly, to understand them from their internal structure, to understand them in the same way as insects, should expect their metamorphosis. For example, whoever should carefully examine *Brassica oleracea,* and afterwards should see *Crambe maritima,* would be quite convinced that *Brassica* and *Crambe* by relationship

("cognatione") should border near one another, and never think other than two so very dissimilar[7] plants should produce similar fructification, would, however, suppose the opposite when the fructification appears in *Crambe,* which differs so very much from that in *Brassica* that it comes close to *Rapistrum maximum rotundi folium monospermum Cornuit,* to such a degree that these two, although dissimilar, more properly are cognate and are themselves associated by qualities, more than the aforesaid, and this the internal structure of the plants, placed in front of our eyes in the fructification, shows.

—Linnaeus (1755a, p. 15)

Thus larvae, effectively equivalent to the vegetative, external part of the plant, could be very similar, masking taxonomically important differences in the internal structure of the plant as manifest in the flowers. Other examples were Compositae with rayed flowers and those lacking rays, but which were very similar vegetatively, including *Conyza bifrons* and *C. raguzina, Bidens cernua* and *Coreopsis bidens,* etc. (Linnaeus, 1755a). Linnaeus observed that such plants were called "Bifrontes" by botanists; the *Conyza bifrons radiata* of the first edition of the *Species Plantarum* (Linnaeus, 1753) became the *Inula bifrons* of the second and subsequent editions. Since the petals, stamens, and stigma were at the same time the internal structure of the plant and the adult plant that became visible after its metamorphosis, this disposed of potential objections that the parts of the fructification, on which classification was based, were transient structures. They were not, because they were manifest during the whole life of the *adult* plant, or at least a good part of that life (see Ray, 1696; Sloan, 1972).[8]

The significance of this set of analogies is clear. This way of visualizing the plant meshed with Linnaeus's statements as to the relative importance for classification of the different parts of the plant. The external form of the plant, its habit, was largely the impression on our senses made by its most obvious parts, the stems and leaves, which were cortical in nature. The habit was comparable to the larva and was a poor guide to taxonomic relationships at the generic level. This is because what is classified is not the larva, crust, or skin—not the vegetative parts of the plant derived from the cortex—but the imago, or fructification, generated by the medulla or the interaction of the medulla with the cortex (see, e.g., Linnaeus, 1762b). It was the inner parts of the plant that were displayed in the flower. Following Linnaeus's basically Cesalpinian appreciation of the principles of life, it is in these parts that the vital principles of the organisms resided (see below), and so it is on them that classifications should be based. The fructification became evident only after the metamorphosis of the plant, the calyx, or cortex, being torn. Of course, although all the parts of the fructification were essential taxonomically, when they fell from the plant the essence of the plant had not been lost, since the

[7]Later (Linnaeus, 1759c) corrected to "similar."

[8]To strengthen the analogy, Linnaeus frequently described the fructification as the "animalcule" of the plant, with the calyx corresponding to the elytra, or wing cases, the petals to the wings, and the stamens and pistils to the genitalia (see also Linnaeus, 1759b, 1760a, 1762b, 1767c, 1776).

medulla, which produced them or stimulated their production, persisted in the seed. Hardly surprisingly, then, the seed, with its corculum nestling between the upwardly growing plumule and the downwardly growing radicle, and enclosed by cortical layers that were "sloughed off" or "molted," was the real seat of life in the plant.

The bud, and indeed vegetative variation in general, was of little taxonomic importance at the generic level (Linnaeus, 1762b). However, as Linnaeus later (1767b, p. 10) remarked, the differentiae of the larvae—that is, vegetative differences—could be used for the names of species since such differences were used in distinguishing between species.

Prolepsis, or Anticipation, and the Comparison of Floral and Vegetative Shoots

Despite the variety of form manifested by the appendicular organs, both within and among plants, there were nevertheless important similarities among these organs. One of the ways of looking at such similarities was the theory developed by Linnaeus in which the growth of the flower, which occurred in a single year, could be equated with several years' growth of the vegetative plant. The two theses in which this subject was most extensively treated are *Prolepsis Plantarum* and *Prolepsi Plantarum* (Linnaeus, 1760c, 1763)—literally, the anticipation of plants. These theses, although with similar titles, differ in the approaches that Linnaeus adopted. In the first (Linnaeus, 1760c), defended by Ullmark, emphasis was placed on the fact that each type of floral organ could be considered as equivalent to a year's growth of the vegetative shoot and were themselves the "shoots" (soboles)[9] of that year's growth. In the second (Linnaeus, 1763), defended by Ferber, more emphasis was placed on what is basically a physiological explanation for the relationship among the different parts of the plant in general, the parts of the branch and bud, and the parts of the flower, as well as the tissues out of which all the parts of a branch, bud, and flower are constructed. Of course, instances that apparently did not fit this general explanation received special attention.

However, the notion of the opening of the flower anticipating several years' growth of the vegetative shoot was itself anticipated in earlier writings. In Löfling's (1749, pp. [1], 4) pivotal thesis a similarity among bud scales, cotyledons, and calyx was noted; all enclosed younger parts of the plant and were forced open, or fell off, as they expanded. The plant growing by vegetative buds was like a polyp, and that growing from seeds ("generatio") more like an animal with eggs (see also Linnaeus, 1746). Linnaeus (1759a) later described three types of reproduction in plants; the third was vivipary, itself a kind of precocious growth (see also Linnaeus, 1760a). The bud was simply a continuation of plant, rather than something new; the seed, however, was entirely new when grown

[9]Linnaeus used the term "soboles" in connection with the development of leaves, sepals, petals, and the like, but these are not branches or twigs, for which he used the words "ramus" or "ramulus." Here the word "sobol" is translated as "shoot," and the word is always in quotes; without quotes, the word is used to mean a young branch.

(Löfling, 1749, p. 4, "continuata" and "propagata"; see also Broberg, 1985). However, as is apparent above, both flowers and vegetative shoots were enclosed in buds, the scales of which fell off, and were actually formed in the preceding year (Löfling, 1749). Flowers in the axils of the scales of a catkin (ament) could thus be compared to small buds in the axils of leaves of a leafy shoot, the latter, however, developing ("germinandis") only in the following year (see also Guédès, 1969). Buds were not found in leaf axils where there are fructifications, hence Linnaeus thought about how the fructification, just like the vegetative plant reduced to rudiments ("in compendium redacta"), could develop from a bud that had undergone metamorphosis (Löfling, 1749, pp. 12, 13).

Thus the fructification could develop a year before comparable structures on a leafy branch. Annual plants, too, were precocious (*ibid.*, p. 12): "If precocious flowers, which may be considered to be unexpanded buds, mature seeds in that year [in which they flower], and the same year are dispersed onto the ground, and may germinate in the following year, you may see nature hastening to open the outer bud scales of the fructification to such a degree that germination from the seed corresponds completely to the germination of leaves [which give rise to the developing leaves of the vegetative bud]; herbs ["herbae"] therefore avoid undergoing both vegetative and reproductive growth at the same time." The seed is in some way the "bud" of the annual plant; perhaps this comparison was in part to circumvent the apparent absence of buds in annuals (see Ray, 1686).

Here we see the idea of anticipation combined with that of the metamorphosis or change of one part into another; this latter concept we shall deal with shortly. Both in turn are combined with intimations of the physiological kind of explanation that Linnaeus would later adopt for them. As Löfling (1749) noted elsewhere in the same thesis, buds were nothing but the vegetative part of the plant contracted because of a deficiency in the vegetative force.

There is a very terse summary of the mature version of the theory of anticipation in the important tenth edition of the *Systema Naturae* (Linnaeus, 1759b, p. 826; see also Guédès, 1969): "The 'shoots' of the *present* year are the leaves; of the *next* are bracts; of the *third* the perianth (calyx); of the *fourth* the petals; of the *fifth* year the stamens, and the stamens being produced (exhaustis), the pistil. These things are clear: of themselves; because of Ornithogalum; luxuriant [growth]; proliferous flowers; doubled flowers and Carduus."

A slightly more expanded account appeared soon after in the edition of the thesis *Metamorphosis Plantarum* prepared by Linnaeus for the collected edition of these theses defended by his students, the *Amoenitates academiae* (Linnaeus, 1759c). It should be noted that this account (see Figure 3) is an addition and is not found in the original version (Linnaeus, 1755a; 1759c, cf. p. 372). Much of this addition was translated (into French) by Guédès (1969), who did not realize that it was not part of the thesis as originally published.

Linnaeus inserted this new section after discussing "budding" and individuality in *Taenia*, polyps, and the like (see also Linnaeus, 1748). After making an analogy between the cerebral and vascular systems of an animal and the medulla and cortex of a plant, he compared the various parts of the flower

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quadrupeda vivipara pullos ſuos generent, qui utero funiculo umbilicali & placenta alligantur, quæ in illis marceſſit, ſed in vermibus, & quidem inprimis *Tænia*, videmus matrem partum ſuum edere, eidemque adhærere, quo ſit, ut pro quavis generatione, novus exoriatur articulus, qui diſtincta eſt vita, ſeu diſtinctum individuum, ut in radice *Tritici repentis*. His intellectis *Polypos* ſeu *Sertularias* inſpicere debemus, qui eodem modo ac Tænia partus ſuos, licet plures, edunt, & iis adhærent, ut ramoſæ plantæ ſimiles evadant; quam primum enim matres moriuntur, indurantur eorum corpora, & truncum vel ramum conſtituunt, adeo ut pulli viventes in ſummitatibus tantummodo ſint, conſimiliter ac in vegetabilibus, in quibus quævis gemma novam conſtituit vitam, licet cum priori cohæreat; ſed fato illi obnoxia eſt, quod, poſt ſemel peractam floreſcentiam vel exuitionem larvæ, nunquam ex eadem, planta aliqua nuda, vel flos proveniat.

► Uti Animalium machina conſtat Syſtemate *cerebroſo* & *vaſculoſo* nutriente, ſic etiam vegetabilium; in his *Medulla* loco cerebri ſ. Medulla ſpinalis & *Cortex* loco vaſorum per quem ſuccus alimentaris deſertur. Ex cortice deponitur quotannis Liber; ex Libro ſit Lignum rigidum loco oſſium. Adeoque hæ duæ partes eſſentiales conſtituunt Larvam plantarum & hæ partes dein mutantur in Florem, tamquam in Inſectum volitans coleoptrato calyce corticali, alatis Petalis e libro licet fixis, maſculis Staminibus e ligno & femineo Piſtillo Medullari.

Quomodo hæc metamorphoſis fiat vel non fiat apertiſſime patet intuenti e. gr. Scillam aut Ornithogalum capenſe. Ubi

a. Bulbus conſtans ſquamis tunicatis, prioris anni relictis baſibus foliorum.

b. Fo-

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b. Folia baſi intra bulbum vaginantia præſentis anni ſoboles & herba ſunt.

c. Gemma minima reſidet intra baſin ſinguli folii in bulbo.

d. Hæc gemma (c) dabit proximo inſequente anno folia, niſi tabeſcat.

e. Si vero hæc gemma (d) protruditur, mediante enato ſcapo, in folia, eodem anno quo priora (b) folia, fiet ſpica.

f. Bracteæ in hac ſpica (e) tum ortæ fuere ex foliorum rudimentis uno anno præcocioribus, adeoque teneræ.

g. Dum Bracteas has (f) concipio uti gemmæ (c) ſquamas, in folia enatas (d), ſequitur etiam quod concipiam in eorum alis hærere alias gemmas minores, ſi bulbus permanſiſſet; Sed ultimæ hæ flores evadunt,

h. Corolla adeoque ſe habet uti gemma tertii anni (g), quæ ideoque duobus annis præcocior exiſtit.

i. Si itidem in ipſa corolla, tamquam in bulbi gemma concipio hærere minores bulbos, videbo hos mutatos eſſe in ſtamina; adeoque Stamina quarti anni ſoboles ſint; imo & piſtillum quinti anni. ◄

Qui naturam inſectorum ſcrutati ſunt, invenerunt, quod ſic dicta metamorphoſis in inſectis, proprie non ſit tranſubſtantiatio, qualem *OVIDIUS* ſibi repreſentavit, ſed tantummodo decorticatio: Et *SWAMMERDAM* clare obſervavit, quod in larva Papilionis Braſſicæ, cum etiamnum in terram reptat, alæ & totus Papilio, ſub ipſo cortice abſconditus eſſet; adeo ut hæc metamorphoſis, denudatio partium tantum eſſet, eodem modo ac in floribus. Si jam flores inſpiciamus, videbimus eos nihil aliud,

Aa 3 niſi

FIGURE 3. Addition to thesis *Metamorphosis Plantarum* (*in* Linnaeus, 1759c, pp. 331, 332; paragraphs between arrows added in this version).

with parts of the adult insect and the particular tissues from which they arose. He then went on to discuss this metamorphosis in the context of the growth of *Scilla* and *Ornithogalum*. He suggested that a bud in the axil of a leaf might produce additional leaves the following year, or it might develop into a spike in the same year that the leaf was produced. The leaves on the spike—the bracts—were tender because they were precocious, representing the leaves of the next year's growth; like other leaves, they bore buds in their axils, but these developed immediately into flowers. The corolla (perianth) was thus the bud of the third year and developed two years in advance, the stamens were the "shoots" of the fourth year, and the pistil that of the fifth year.

The details of the equivalence of the several parts of the flower with a particular year's growth might differ, as with the version in the *Systema Naturae* just mentioned, but the principle was the same. Linnaeus equated each morphologically different part of the flower (or inflorescence) with one year's growth. Since both *Scilla* and *Ornithogalum* lack bracteoles and have a perianth rather than a readily distinguishable calyx and corolla (see below), the differences in the two versions of prolepsis outlined relate to differences between these monocotyledons and the more common arrangement in dicotyledons. A similar variation of this basic theme is found in Linnaeus's explanation of double flowers in the Compositae: the involucre represented the "shoots" of year two; the receptacular bracts, those of year three; the pappus, year four; the corolla, year five; and the petaloid pistil, year six (Linnaeus, 1760c).

These two theses on prolepsis thus represent the extended justification and discussion of the mature form of the theory of anticipation. There was a close parallel between the growth of the vegetative branch and that of the flower "wherever leaves are found, there between the substance of the cortex is the fiber of the medulla"; ". . . the cortex produced leaves, thus leaves are nothing other than "shoots" advanced from the cortex and can produce new life" (Linnaeus, 1760c, pp. 4, 11). In the flower, of course, the medulla produced bracts and calyx with cortex, stamens with lignum, and so on; all these structures were basically cortical in origin. Within "the substance of the cortex" (e.g., Linnaeus, 1763, p. 7), which made the floral organs, was to be found the pure medulla in the pistil; in buds, imbricate leaves enclosed the medulla. In both vegetative and floral buds the leaves were associated with buds (but see below). "The tree (*sic*) then produced the flower, nature having anticipated the progeny of five years then producing together [and] forming from budded leaves ("foliis gemmaceis"), bracts, calyx, corolla, stamens, and pistil, and the seed filled up with granular medulla terminating the life of the plant" (Linnaeus, 1767b, p. 9; see also 1763). Note, however, that as with the earlier simpler equation of "tissue" types with different parts of the flower, the parts of the flower involved in prolepsis do not correspond exactly to the seven parts of the fructification that provide the natural characters of genera—calyx, corolla, stamen, pistil, seed, pericarp, and receptacle (see above and TABLE 1). Also, the cortex proper is involved in two years' growth, the other tissues in one.

Linnaeus noted that prolepsis occurred in some animals; in *Volvox globator*, which he included in the Zoophyta (the sixth and last order of the Vermes, in the animal kingdom; see below), he described a comparable series of generations as being visible inside the body of the minute adult (Linnaeus, 1758) and a similar phenomenon was known in species of *Aphis*. Anton van Leeuwenhoek was the first to note what he thought were "seeds" in *Volvox* in 1700 (see Dobell, 1932). Further, the figure five in the five years of the mature theory of anticipation was in line with Linnaeus's favored quinarian numerology (e.g., Jonsell, 1979; Lindroth, 1983; Broberg, 1985).

But there is a tension in Linnaeus's reasoning here, at least to a twentieth-century reader (Guédès, 1969). Linnaeus did not distinguish clearly between axillary and terminal buds but considered that all buds occurred in the axils of leaves of flowering plants; he had no notion of a terminal bud continuing the growth of the stem (see Löfling, 1749). Thus if a flower bud really represented six years' growth, the parts of the flower would come from a series of buds successively borne in the axils of the leaf or leaves of the preceding years' growth, and this is how Linnaeus (e.g., 1760c) discussed that relationship. All the parts of the flower would then be opposite one another. However, Linnaeus (e.g., 1751a, pp. 57, 61) knew that the sepals and petals, at least, alternated in their positions.

There are additional complications caused by attempts to equate each year's growth in vegetative branches with a particular tissue (see FIGURE 2B). Linnaeus

(1763) discussed the detailed structure of the vegetative bud and compared it to that of the flower in the thesis *Prolepsi Plantarum*. The leaves of the first (current), second, and third years came from the cortex, those of the fourth year from the liber, and those of the fifth from the wood. For the leaves of the sixth year, he invoked membranes almost touching the medulla, which he compared to the meninges surrounding the central nervous system of vertebrates. Of course, the sixth year's growth, or the "shoots" of the sixth year, corresponding to the pistil in the flower, could not be the medulla itself, because the medulla was needed to continue the growth of the shoot, whereas in the flower the medulla could be used up in the formation of the pistil, since with flowering the shoot that bore the flower died.

As Linnaeus (*ibid.*, p. 11) went on to say, "Whenever the budded leaves of the first year, which are outside, develop into a branch with its leaves and buds, then as much medulla [as remains] in the axils of the leaves of the sixth year, which are concealed in the intimate shades of the plant, protrudes as the new budlet rudiment (nova protrudit rudimenta gemmulacea) for the seventh year, and thus growth is prolonged" (cf. Guédès, 1969, p. 338; translation of "protrudit" as the ambiguous "produit"). The protrusion of the medulla beyond the cortex agrees with the ideas Linnaeus expressed elsewhere (see above) of the medulla pushing upward and outward and forcing the more rigid cortex apart; continuation of growth is by the medulla in the ultimate (sixth) year's budlet itself budding. Since the mature leaves are always cortical in origin, although this is not always clear in Linnaeus's writings (Guédès, 1969), the development of the vegetative bud described above is at some variance with the normal pattern of tissue development. The inner leaves effectively have to change their nature from wood to liber and then to cortex before they expand, and this direction is the reverse of that in which the tissues develop in the stem.

The Relationship between Plant Parts

With Linnaeus, as with later proponents of the foliar theory of the flower, the analogy between floral and vegetative shoots is connected with that between all appendicular organs. It is not clear which analogy came first to Linnaeus, although the evidence suggests it was the second (see below). Evidence for the equivalence of all lateral organs came largely from the nontaxonomic findings of teratology (note that Sachs (1890) somewhat underrated this aspect of metamorphosis).

A number of interesting abnormal phenomena were early discussed by Linnaeus, although not initially from the point of view of interchangeability of plant parts. Thus in a double flower ("flos luxurians") some parts were multiplied and others destroyed; there might be many petals but few stamens, yet no interconversion between the two was noted (Linnaeus, 1736a). The calyx and corolla sometimes could not be sharply distinguished since in a number of taxa, including *Daphne* and *Ornithogalum*, they formed a single body. This was green and tough on the outside, so showing its calycine quality, and thin and colored on the inside, due to its corolline nature (Linnaeus, 1738, in a discussion of Cesalpino's work; see below). This arrangement is particularly common in spring-flowering plants, and it was later suggested (Löfling, 1749; see also above) that in such cases the substance of the liber did not draw back or separate from the cortex.

There was abundant evidence for the basic similarity of appendicular organs in the changes and intergradations manifest in the various terata, or growth monstrosities, known to Linnaeus and his contemporaries, information on which was summarized in the thesis *Metamorphosis Plantarum* (Linnaeus, 1755a). Guédès (1969) gave a particularly thorough analysis of this aspect of the "metamorphosis" of plants. These terata included doubled flowers, in which the stamens, and sometimes also the pistils, were changed into petals, resulting in sterility (Linnaeus, 1751a, 1755a). Extreme changes also occurred when whole flowers, series of flowers, or even a leafy branch bearing flowers, were produced from the pistil of a simple flower or the receptacle of an aggregate flower like a scabious or a thistle; this is the phenomenon Linnaeus (1751a) called proliferation. Galls and other kinds of insect infestation provided similar evidence of metamorphoses—*Pistacia* produced long, purple follicles, *Cerastium,* imbricate capitula, and so on (Linnaeus, 1755a). In such terata organs changed their form, and such changes, appropriately interpreted, gave evidence at the same time of the potentiality, nature of, and relationships between organs. Hence, despite the fact that petals were not produced directly from plain cortex, they were interchangeable with—and in some way fundamentally the same as—leaves, which were.

Since the liber and the wood were derived from the cortex, it is perhaps hardly surprising to see that under the appropriate "physiological" condition—excess of sap—they could become plain cortex again (see Guédès, 1969). This leads to the other major line of argumentation bearing on the relationship between plant parts, which can loosely be described as a physiological-balance theory of development. Much nutriment led to the production of leaves, or more leaflike structures, while less nutriment caused flowering, or flowers with less leafiness. This argument was also in evidence early; the opening questions of the thesis *Gemmae Arborum* (Löfling, 1749; see also above) seem to expect a physiological answer, and in the important addendum to the *Philosophia Botanica* entitled "Metamorphosis Vegetabilis" (Linnaeus, 1751a, p. 301, translated in part below; see also Celakovsky, 1885, and Guédès, 1969), the explanation for the rudimentary theory of anticipation advanced two years before by Löfling is expanded in terms of such physiological ideas (it should be remembered that Löfling was acting as amanuensis for Linnaeus during the writing of the book):

> Buds or *budlets* or *flowers* or both are fertile.
> The plumule of the seed is often terminated by a flower or bud.
> The principle of *flowers* and *leaves* is the same.
> The principle of *buds* and *leaves* is the same.
> The bud contains rudiments of leaves.
> *Stipules* are appendices of leaves.
> The *perianth* is made up of connate rudiments of leaves.
> By ("derivato") diverted nutriment to the scales of an ament, the destroyed florets are changed to *Leaves.*
> By nutriment diverted to the florets of an ament, the leaves are made *Calyces.*
> Moderate growth produces flowers from the terminal leaves.

This style of explanation was elaborated over the next 15 years (see especially Linnaeus, 1763). It was a well-established horticultural observation, and several times commented upon by Linnaeus (e.g., 1755a, 1760c, 1762a), that plants in fertile ground were wont to branch profusely and produce lots of leaves but few flowers. When the cortex was well nourished, the medulla could not emerge (Linnaeus, 1759a). In poorer and especially drier conditions this relationship was reversed, with less vegetative growth and more flowering. Similarly, plants (such as species of *Dianthus, Papaver,* and *Anemone*) that produced flowers with numerous petals when grown on good soil bore simpler flowers with fewer petals when grown in poorer ground (e.g., Linnaeus, 1755a, 1760c). With an excess of the descending, vegetative force, either more leaves or more petals resulted (petals, of course, although leaflike, were derived from the liber, not the cortex itself; leaves were directly derived from the cortex). As the vegetative force became weaker, the activity of the ascending, generative force in the medulla became more evident; there was freer movement ("propulsioni") in the medulla, the cortex was weaker, and so the medulla emerged further from the cortex and produced flowers.

The general balance theory extended to taxa like *Lilium bulbiferum* and *Dentaria,* where plants with bulbils did not set seed (e.g., Linnaeus, 1763); vegetative forces were again in excess. The different sexes of flowers could in part be at least similarly explained; in male flowers the medulla found its way through the cortical substances but did not have the force to expand into the pistil, dying off or drying out (Linnaeus, 1763).

There is thus abundant evidence that Linnaeus envisioned the fairly ready transition between the different parts of the flower. (This differed from the situation in animals, where in one ambiguous passage Linnaeus (1760c, p. 19; see also Guédès, 1969) suggested that a liver could not change into a heart, or a heart into a stomach; each had its own nature ("sed singula suum retinent principium").) Nevertheless, although transitions occurred, intermediate structures on normal plants were uncommon; they were varieties, variations from the taxonomic or essential norm that depended on fixed and discrete gaps between both the organs of plants and the taxonomic groups.

The situation was not so clear when the pistil was considered; it was normally medulline, yet in doubled flowers it could become petaloid-cortical. Linnaeus suggested that the pistil was indeed covered by a very thin layer of cortex, and it was this that developed and made the pistil—the "shoots" of the sixth year—on occasion foliaceous. However, when this was the case, there was nothing—i.e., no medulla—present in those "leaves" ("Quod si ulterius pistilli mutationem in folia ostendere foret animus . . ."—Linnaeus, 1760c, p. 18). Medulla and cortex were not interchangeable, yet the largely medullary pistil could still be the leaf of the last year in the proleptic series. This version of the development of the flower is similar to that of the vegetative bud discussed above, with "special" tissue of cortical origin, yet not part of the normal series of tissues of cortical derivation, giving rise to the leaves of the ultimate year.

The Cortex-Medulla Theory and Hybridization

The cortex-medulla theory also played an important role in Linnaeus's ideas on hybridization. In normal reproduction the medulla, the internal structure of the plant, its essence, was effectively continuous through time and successive generations since creation because it remains unchanged in the seed (Linnaeus, 1759a). Or, more accurately, the pistil, derived from the medulla, was unable to lay the foundations for the life of the new plant until the woody essence of the stamen had been absorbed by the medullary humor of the pistil (Löfling, 1749; see also above). Later Linnaeus (1767b; see also 1759a) talked about the copulation of the "cortex externa" with the medulla, the medulla in this case being compared to nerve fibers, producing the new life of the plant. Thus the woody essence from the stamen, representing the cortex, and the medulla, from the pistil, were both represented in the seed.

After 1747 in particular, Linnaeus became much interested in the phenomenon of hybridization, although it took him about ten years to develop his views on this subject (Larson, 1971). Excellent summaries have been provided by Bremekamp (1953), Hagberg (1953), Hofsten (1958), Larson (1968, 1971), Stafleu (1971), and Broberg (1985), while Zirkle (1935) included extensive translations of Linnaeus's writings on hybridization. In hybridization the constancy of species form required for Linnaeus's taxonomic system would appear to break down. There is, however, less conflict when such simple hybridization is explained in terms of the cortex-medulla theory. As Linnaeus saw it, hybridization was like any other fertilization event, with involvement of the stamen, basically cortex, and the pistil, pure medulla. The results were perhaps even predictable. Although the hybrid might resemble the father in overall appearance, "with regard to the inner medullar substance and fructification it is the image of the mother" (Linnaeus, 1771, p. 107; see also 1751c, 1759d, 1760a, 1762b) and was thus more likely to be classified in the same genus as the mother (see also Hull, 1985). In an addition to the thesis *Plantae Hybridae* (Linnaeus, 1756a), the analogy between larvae and the vegetative part of the plant was drawn (see above), implicitly suggesting a comparison between the male contribution and the nonessential covering of the metamorphosing insect. As Hofsten (1958, p. 80) aptly remarked, "the new species were the old ones in new array." They were the old ones because they had the same medulla and were in the same genus; they were in new array because they had a different cortex. There were, however, possible taxonomic problems for Linnaeus when infrageneric hybridization was considered; varieties, and variation in general, might be the result (Linnaeus, 1762b).

Toward the end of his life, Linnaeus developed larger ideas as to how much plant diversity could be explained by hybridization (see particularly Hofsten, 1958; and Larson, 1971). The details of these complex theories need not concern us here, but the basic results of hybridization at any level would be expected to be the apparent physical dominance of the father but the taxonomic dominance of the mother. God created organisms with medulla covered by the principles of the various kinds of cortex; these were the ordines naturales. Successive hybridizations produced genera, species, and varieties (Linnaeus, 1764; see Bremekamp, 1953, and Larson, 1971, for translations). Bremekamp (1953) calculated that up to 216,000 species could be produced by this whole process—rather more than the 10,000 or so Linnaeus believed existed. During these hybridizations, what was originally undifferentiated medulla is gradually modified by the different cortices that God had created.

Bremekamp (1953) saw this hybridization theory (as in Linnaeus, 1762b, 1764) as justifying the levels of the Linnaean hierarchy. He thus suggested that it not only explained the generation of taxonomic *diversity* in plants, but also the fact that there was a taxonomic *hierarchy*. However, it should not be forgotten that there are five levels of the Linnaean hierarchy—the four just mentioned, as well as the classes into which the ordines naturales were grouped. Also, there were suggestions that hybridization provided Linnaeus with a reason why his families (ordines naturales) could not be defined. Problems surrounding the definition of such families were not simply caused by the tension between the recognition of such families by their habit and their definition in terms of fructification characters. Hybridization might even lead to the recombination of these fructification characters, which would mean that they would not be restricted to any particular family (Malmeström & Uggla, 1957; cf. Larson, 1971; see also above). But hybridization between species or even genera would not necessarily disturb the economy of nature (Atran, 1990; see also below); the properties of congeneric plants are largely the same and are unaffected by hybridization (Linnaeus, 1762b). Finally, if all possible hybrid combinations are produced, the "form" that taxonomic diversity takes is likely to be very regular, and depending on the nature of the interactions of cortex with medulla, without any particular gaps (Eriksson, 1983), a subject to which we now turn.

Continuity and the Cortex-Medulla Theory

Linnaeus, although believing both species and genera to be discrete, considered that at higher taxonomic levels there were no particular gaps.[10] Linnaeus's great interest in the *peloria* variant of *Antirrhinum* (see the thesis *De Peloria*, defended by Rudberg; Linnaeus, 1744) shows his concern over change that transgressed established boundaries. *Peloria* was an example: how could a genus arise *de novo*, since genera were immutable and discrete? But *Peloria* could be fitted into his general taxonomic scheme of discrete, generic-level entities. Additionally, in *De Peloria* the intermediate nature of corals, Abraham Trembley's work on polyps, and the production of wingless aphids by winged aphids also received attention. All these phenomena were later integrated with his ideas of systematic continuity at higher taxonomic levels, although it was perhaps not so much the change from winged to wingless in aphids that was emphasized by the later Linnaeus, but the way in which they reproduced.

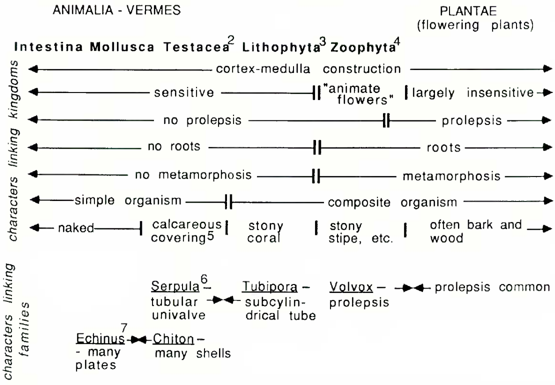
[10]Broberg (1985) rightly noted that although Linnaeus crossed out "natura non fecit saltus" in his own copy of the *Philosophia Botanica*, this was simply an editorial correction; the phrase was repeated twice in the same section, and Linnaeus allowed the second mention to stand.

The comparison of the vegetative bud with a polyp, and of seeds with an egg-bearing animal (e.g., Linnaeus, 1749), was important in heralding the integration of the cortex-medulla theory with ideas of continuity (for a good treatment of this, see Broberg, 1985). Practically all the different aspects of the theory were involved. The thesis *Animalia Composita* (Linnaeus, 1759a) presented the justification for Linnaeus's remodeling of the arrangement adopted in the last part of the animal kingdom in the tenth edition of the *Systema Naturae* (Linnaeus, 1758), a rearrangement that can be understood only in the context of the cortex-medulla theory. As noted above, Linnaeus frequently compared the medulla to part or all of the nervous system of animals, and in the thesis *Animalia Composita,* for example, animals were said to have the same general cortex-medulla construction as plants (see also Linnaeus, 1759d; Lindroth, 1983; Broberg, 1985). The medulla of plants was equivalent to the spinal medulla of animals, that is, to the spinal cord itself. Thus all organisms possessed the cortex-medulla type of construction. However, the constraint exercised on the medulla spelled one of the differences between most animals and plants. The latter were composite organisms because the medulla was able to push through the cortex and form buds; in animals, the medulla remained strictly enclosed by cortex, so buds could not form and the organism remained simple. Plants were branched, and this branching was the manifestation of the inherent multiplicative property of the medulla (see below). But in worms and some other animals, there was also no constraint to the medulla, no hard vertebral column, and so the medulla could escape in the same way as it did in plants (Linnaeus, 1759a). Thus a single articulation of *Taenia* had life, just as a single articulation of the root (rhizome) of *Triticum repens* could give rise to a complete new plant (Linnaeus, 1767a). Composite animals were placed next to flowering plants in Linnaeus's scheme of things (see Table 2).

In Table 2, the distribution of this feature along with others that come from plant and animal construction are superposed on Linnaeus's grouping of the Vermes (see Linnaeus, 1758). The class Vermes ended with three orders. The first, the Testacea, were bivalve and gastropod mollusks in which a single animal was covered by a hard shell. The next group, the Lithophyta, were "composite molluscan animals, sprouting out from strong underlying coral in which they are grafted and which they build" (*ibid.,* p. 789). A shell is there, but in this group the animals are "composite," being organically connected. Linnaeus described the animals involved as nereids, which he would probably have put in the order Intestina if they had not been enclosed in stony matrix, or as hydroids, which he would likely have placed in his last order, the newly circumscribed Zoophyta, if they had been free living (see Linnaeus, 1745, for earlier arguments as to whether corals were plants, animals, or stones, and if animals, whether they were to be classified by the coverings or the organisms contained). The Zoophyta consisted of "composite flowering animals with an animated body (stirps vegetans)" (*ibid.,* p. 799), one of its members, *Hydra,* being described as a sensitive flower (note that the Zoophyta were originally placed with plants—e.g., Linnaeus, 1737).

These three orders, particularly the Zoophyta, were all more or less anomalous in the context of typically animalian features. The Zoophyta in particular

TABLE 2. **The Linnaean scala at the juncture of animals and plants.**[1]



[1]This table depicts the distribution of different features "separating" animals and plants. Most of them also occur in some, but not all, members of the Animalia-Vermes and sometimes isolated elsewhere as well—for example, prolepsis in *Aphis* (Animalia-Insecta-Hemiptera). The vertical lines give some indication of the degree of separation between the groups afforded by each feature. Also shown are some bridging genera that blur the lines of separation between families, making smaller-scale linkages.

[2]The animals inhabiting the shells of the Testacea are usually referred to molluscan genera, but *Teredo* belongs to the Intestina (see also Linnaeus, 1771b, for problems in classifying shells; and Lindroth, 1983, for references).

[3]The animals inhabiting the Lithophyta belong either to the Mollusca (*Nereis*) or the Zoophyta (*Hydra*).

[4]The "flowers" of the Zoophyta are usually referred to *Hydra,* itself a zoophyte, rarely to *Medusa,* a mollusk.

[5]Details of the various stony and woody coverings differ, but the fact that these groups all have coverings of one sort or another is important.

[6]*Serpula,* the last genus in the Testacea, is the only one in which the animal is described as being a *Teredo*; this may be in part because of the similarity of a *Serpula* "shell" to the calcareous lining of an exposed burrow of *Teredo. Serpula* in Linnaeus's sense contains wormlike annelids that, if free living, would probably have been placed by Linnaeus in his Intestina. *Serpula penis,* however, is a lamellibranch mollusk; paired shells can be seen at the end of the tube (K. Boss, R. Turner, pers. comm.). The genus adjacent to *Serpula, Dentalium,* has a tubular shell and is included in its entirety in the Mollusca today (see also Dodge, 1952, for the taxa included in the Testacea; Winsor, 1976, for a description of serial sequences in Linnaeus's insect classification.

[7]Linnaeus did not mention the distinctive, rather platelike construction of many echinoid coverings here, but these are very evident. The general arrangement of the Testacea is: first, genera in which the shells have many valves, then genera with two valves, then genera with one spiral valve, and finally genera with one valve that is without a regular spiral (see also Cain, 1983).

were constructed like plants, yet they were more obviously like animals in their behavior. They often had roots; they were generally caulescent, with life multiplying in branches; they had buds that could be removed; and they metamorphosed into an animate flower that had the power of voluntary movement and that itself changed into seed-bearing capsules (Linnaeus, 1758, p. 643). Although the Zoophytes lacked leaves, Linnaeus (e.g., 1751b) suggested that the leaves of a plant might indeed be organs of motion that were passively moved by the wind. The articulations of the Zoophytes were the "exuviae" of the animal, solid cortical tissue, the result of a process similar to that by which the cortex of the bark changed into solid wood (Linnaeus, 1759a). Linnaeus noted that the Zoophyte *Hydra* behaved like *Salix* in that its separated buds could grow into independent organisms;[11] the ability of *Salix* cuttings to grow so readily provided him with a good example of the role of the medulla in vegetative growth, just as its catkins provided an early example of prolepsis. The last genus in the Zoophyta, *Volvox,* included *V. globator,* which as we have already noted showed yet another plantlike feature, prolepsis. To summarize, the species placed in the Zoophyta and Lithophyta were complex organisms in which the notion of individuality developed for higher animals was inappropriate, but which were more plantlike in this respect as well. The Zoophyta even included *Taenia,* the tapeworm, which had earlier been classified in the Vermes-Reptilia (Linnaeus, 1756; of the Vermes-Intestina of Linnaeus, 1758), but which Linnaeus came to believe was also a composite organism, the articulations of which had internal flowers!

TABLE 2 shows clearly the nature of Linnaean continuity with an overlapping, catenalike distribution of characters, all of which come from Linnaeus's understanding of the cortex-medulla theory; we can find no other relevant characters. It is interesting that both Linnaeus (e.g., 1759a, p. 4) and Fabricius (*in* Giseke, 1792, pp. [2], 4) used the word "catena" in the same context of continuity. Plantlike features are found in many animals, so making the distinction between the two somewhat a matter of taste. As can also be seen from this table, features of plants do not simply overlap into animals, being found throughout major taxonomic groups. They may occur in only a *part* of these groups—a part that Linnaeus placed immediately adjacent to groups in which these features were constant. In a world in which continuity rules, "groups" are circumscribed by more or less arbitrarily selected characters and cannot be defined by covarying characters (see also Lamarck, 1778).

Note that in the Testacea and Lithophyta, Linnaeus gave the general identity of the organism inhabiting the hard covering the particular nature of which defined these groups—e.g., "Animalia Teredo." In the Zoophyta there are comparable references to these organisms, but as flowers: for example, "Flores

[11]Abraham Trembley's then recent, but already celebrated, work on *Hydra* paid great attention to its capacity to grow and regenerate (e.g., Trembley, 1744). Dawson (1987) discussed Trembley's work in some detail and showed that some of his experiments were performed because of his beliefs that *Hydra* was a plant and that plants were inside-out (not upside-down) animals. Dawson also detailed the impact of Trembley's work on Charles Bonnet, who, unlike Trembley, interpreted this and other evidence as support for the existence of a Ladder of Natural Beings. Bonnet's (1745) arrangement of continuity along this ladder differs in detail from that of Linnaeus.

Medusae" and "Flores Hydrae." It is interesting to see that the actual metamorphosis represented by the appearance of those flowers was interpreted as being more like that of plants than that of insects, since the zoophyte flower did not separate from its stalk, unlike the imago of the insect (Linnaeus, 1762b). From the Zoophyta with their "flowers" and largely vegetable (flowering-plant) type of construction, it was of course a short step to the flowering plants, the next group in the scheme of things. It should be remembered, however, that Linnaeus (e.g., 1766a) considered the Zoophyta to be the link among all *three* kingdoms, the mineral kingdom included.

Unfortunately, it is impossible to follow the linkages within flowering plants by studying the arrangement of plants in the *Genera Plantarum* or the *Species Plantarum,* since both followed the sexual system that did not represent natural relationships as Linnaeus saw them. The fragments of a natural arrangement that Linnaeus (e.g., 1738, 1751a) produced lack the characterization of the groups recognized that might allow the kind of analysis presented here to be taken further. However, the partially characterized groups in Giseke (1792) may be susceptible to such an analysis, although the form that the continuity is likely to take will probably not be linear, as the illustration of the relationships of these groups (*ibid.*, figure facing p. [623]) suggests. Of course, any "combinatorial" hybridization of cortex and medulla (see above) is also unlikely to generate linear continuity. Although Linnaeus grouped genera into natural families, from Giseke's figures it is clear that some genera bridged gaps between groups; there were also plants not yet discovered that might fill the gaps. In addition, a property of "natural" groups in a world of continuity needs emphasizing here. Such groups contain a portion of the real (continuous) order yet are artificial in that their boundaries are not evident in nature. That our groups have more or less "real" boundaries should not blind us to the distinctive nature of Linnaean higher taxa (as well as those of Lamarck and De Jussieu).

VOLVOX CHAOS, CHAOS PROTHEUS, AND UNRESTRAINED MEDULLA

The last species mentioned in the first volume of the tenth edition of the *Systema Naturae* (Linnaeus, 1758) is *Volvox chaos,* which Linnaeus found to lack definite form, in this respect being "more inconstant than Prometheus (*sic*)" (*ibid.*, p. 821). In the twelfth edition of the *Systema Naturae,* Linnaeus (1767b) again remodeled the last part of the Zoophyta, and he added the genera *Furia* and *Chaos,* the latter including *Chaos protheus* (*sic*), the erstwhile *Volvox chaos,* and other minute organisms. (The word "chaos" has several connotations: Chaos was a primordial world of disorder, formlessness, and confusion; Linnaeus's genus *Chaos* was certainly all three.)

Linnaeus (1767a) included details of recent discoveries of submicroscopic life in the thesis *Mundum Invisibilem.* He discussed Otto von Münchhausen's work on fungi both extensively and with approval. Von Münchhausen had claimed to have found animalcules developing from the seeds of such fungi as *Ustilago, Lycoperdum,* and *Agaricus,* so perhaps making fungi animal, rather than plant, in nature.[12] Linnaeus (1767a) speculated that fungi might better be put in a new kingdom, perhaps along with polyps and infusoria ("Moleculae vivae"). He (1767b) placed the animalcules coming from fungi in the genus

Chaos (as *C. fungorum* and *C. ustilago*), *Chaos* being the genus that contained infusoria and animalcules of all sorts. Linnaeus even thought some diseases were perhaps caused by organisms that should be placed in this genus. To Ramsbottom (1941, p. 297) this recognition of the genus *Chaos* represented a "lamentable lapse" on Linnaeus's part: "So acute in his sense of affinities, so sure footed in so many different fields, Linnaeus here came sadly to grief." But Münchhausen's findings must first be interpreted from Linnaeus's point of view (for other literature on Münchhausen, see Ramsbottom, 1941; Ainsworth, 1976; Broberg, 1985). *Chaos* itself fitted readily into the general superstructure of the cortex-medulla theory.

This new kingdom to which Linnaeus alluded was intermediate between the animal and plant kingdoms ("neutrum seu chaoticum vocetur"—Linnaeus, 1767a, p. 12). It was, however, not so much in disorder as made up of organisms lacking precise form. Thus the last scholium in the thesis addressed the issue of whether these smallest animals were pure medulla, lacking an organic body. Pure medulla might be the seat of life, yet it was formless, or at least without constant form; only when constrained by and interacting with the cortex was definite form generated.

In addition, that Münchhausen's fungi should develop into microscopic worms would surely find ready resonance in Linnaeus since he had earlier (1751a) noted that the fungi were in classificatory chaos, with specific and varietal limits being indistinct because of the lack of constant form in these organisms. Perhaps the problem with fungi was that they lacked much hard cortex; to Giseke (1792), probably reflecting Linnaeus's later thoughts on the subject, this lack certainly explained how fast fungi grew (here Giseke is apparently reporting on his studies with Linnaeus in 1771). The variability of fungi, the greatest of any plant, again occasioned comment. It was almost to be expected that classification, which depended on constant morphology (this in turn depending on the interactions of rigid cortex and medulla), would be so difficult in the fungi.

Animation was the major characteristic of life, a characteristic that resided in the medulla. Linnaeus (1767a, p. 19; see also above) even considered the possibility that the medulla of the inanimate plant itself might be animated, although being constrained by the cortex it could not show this property. Small wonder that when organisms were made up of pure medulla they showed active movement and sensitivity, but not constant form.

Linnaeus toyed with the idea that the relationship between the plant and animal kingdoms was similar to the metamorphosis that occurred in the development of plants and insects, that of the plant in particular occurring during prolepsis and the shedding of its covering ("ut viderentur ipsa naturae adyta penetrari detegendo *prolepsin* transformatum per antipraegnationem"—Linnaeus, 1767a, p. 20). Zoophytes also showed this metamorphosis, but becoming

[12]In the eighteenth century, fungi growing out of insects or other animals were discovered. Linnaeus (1753) initially included these fungi in *Clavaria,* but species like *C. militaris* were eventually transferred to *Cordyceps.* Although there was considerable debate as to whether or not such "vegetable flies" or "vegetable wasps and plant worms" (Cooke, 1892) provided evidence of heterogenesis, they do not seem to have played an important role in that element of Linnaeus's thinking under discussion here (see Lütjeharms, 1936; Ramsbottom, 1941).

more like animals in the process ("per metamorphosin abire in animalia, quemadmodum plantae in flores" (*ibid.*)); hence, plants could possibly metamorphose into animals—witness Münchhausen's findings. So prolepsis, metamorphosis, and the cortex-medulla theory were adequate to the challenge presented by this unexpected microscopic world, although clearly an even larger issue is raised—that of the nature of the generation of life itself (Broberg, 1985). Preformation was, however, clearly not involved (see also Farley, 1982, but cf. Goethe, 1891, p. 322).

Goethe, De Candolle, and Metamorphosis

Goethe developed his ideas on the relationship between the appendicular organs of plants in his *Versuch die Metamorphose der Pflanzen zu Erklären* (Goethe, 1790; additional references are to the translation by Arber, 1946) during his travels in Italy, and especially in Sicily in early 1786.

On the surface there is general congruence between Linnaeus's and Goethe's views on plant form, both involving a fundamental similarity between organs of the plant that appeared at first sight distinct. Goethe emphasized annual plants (Arber, 1946), while Linnaeus stressed perennials and trees, although as we have seen, the latter did not entirely ignore annuals (to Goethe, Linnaeus's ideas seemed to mean that annuals were plants originally destined by nature to live for six years). In his almost exclusive consideration of the above-ground, appendicular parts of the plant, Goethe effectively deemphasized Linnaeus's downward, vegetative movement, being little concerned with the root, but so was Linnaeus in his morphological writings. Goethe considered that the generative tissue of the plant was the liber, not the medulla, and that the various parts of the flower represented a series of expansions and contractions of tissue under the influence of an ever-more-refined sap. He saw all seven appendicular parts of the plant (leaves, calyx, corolla, stamens, style, fruit, and seed) as representing six steps, three successive expansions and contractions: stem leaves (expansion) and calyx (contraction), petals (expansion) and sexual organs (contraction), and fruit (great expansion) and seed (great contraction). This idea of the development of the plant is more complete than that in most versions of Linnaeus's theory of prolepsis (but cf. Linnaeus, 1746), all parts of the plant being involved; Goethe also did not discuss particular tissues not being responsible for producing particular organs. Goethe emphasized the interchangeability of floral and vegetative organs, citing evidence very similar to that given by Linnaeus and placing great weight on teratologies like doubled flowers and on transitional organs. For Goethe, the group of structures that Linnaeus called nectaries played an important role both in the progressive refinement of the sap of the flower, refined sap being needed for the production of the sexual organs, and in demonstrating intermediacy in form between the petals and the stamens.[13]

[13]Interestingly, others found Linnaeus's term "nectary," which he used in a taxonomic context but with an almost physiological definition (e.g., Linnaeus, 1751a), to be unsatisfactory for their largely taxonomic concerns. Linnaeus (1762a) listed 18 different kinds of nectaries in addition to other glandular structures outside the flowers; all secreted nectar, or apparently did. However, his contemporaries and their immediate successors thought that there should not be a single term, "nectary," since these structures were very different in nature (see, for example, Turpin, 1815; Stevens, 1984a).

The main difference between Goethe and Linnaeus is less in the detail of their explanations of how tissue and form were generated, although there are substantial differences, and more in the role these ideas played in their thought. The two belonged to entirely different intellectual generations. At the risk of oversimplification (see below), it can be said that Linnaeus ultimately needed constant and discrete characters to be able to classify, and his theories on metamorphosis, prolepsis, and hybridization involve a fairly precise and circumscribed causality of form. Goethe, on the other hand, adopted a more Neoplatonic approach, seeing unity in nature, indeed in life as a whole, and was looking for ideas behind (or in front of) manifest form, more real than the form itself. That form might intergrade was not worrying but the reverse. Goethe (1891, 1901) himself considered Linnaeus's approach limited.

There was a further connection between the two men. When Goethe developed his ideas in 1786, he had with him an old edition of the *Genera Plantarum* (Goethe, 1890; probably ed. 4, published in 1752). He had also apparently read the *Philosophia Botanica* (Mueller, 1952), in which, as we have seen, Linnaeus's ideas on metamorphosis were clearly, if concisely, expressed. Goethe of course made repeated reference to Linnaeus when he later wrote the *Versuch die Metamorphose der Pflanzen zu Erklären.* Ideas of metamorphosis are generally evident in Linnaeus's work from the 1750's onward. Goethe's actual discovery of the idea of metamorphosis was, according to his own accounts (e.g., Mueller, 1952), independent.

De Candolle (e.g., 1827, Vol. 1; see also Guédès, 1972), who also developed the notion of the fundamental similarity of all the appendicular parts of the plant, did so largely independently of both Goethe and Linnaeus; he could not even read German. His ideas are best expressed in his *Théorie Élémentaire* (1813) and especially in the *Organographie Végétale* (1827). In the former the evidence for this similarity came from the intermediacy of form of different organs and the relationship between parts in "normal" flowers, but in the latter he made more of evidence from teratology and also noted briefly the effects of cultivation and the amount of sap on whether or not a plant would flower. He was early (e.g., 1807) interested in the doubling of flowers. He incorporated some of Goethe's terminology into his work but apparently largely ignored Linnaeus. This was perhaps because it had long been evident to De Candolle that Linnaeus's notion that the pistil was made up of pith could not be true of the monocotyledons (De Candolle's "Endogens"). De Candolle (*in* Lamarck & De Candolle, 1805) and others considered that the monocotyledons had no pith. (Compare Lamarck, 1778—he considered pith to be essential for life, its death with age causing the death of the individual.) Although he largely used the same kind of evidence for establishing the similarity of appendicular parts of the plant as did Linnaeus, he did not cite Linnaeus; the approach of Grew and Malpighi was clearly more congenial to him.

De Candolle was perhaps primarily a taxonomist; his morphological work helped his taxonomic studies in that it made the often variable and deceptively simple structure of the flower more comprehensible and regular to him and helped in the development of his ideas of floral "symmetry" (not the same as "type"—Stevens, 1984a). De Candolle's emphasis on the similarity of sepals, petals, leaves, and the like was immediately seen by his contemporaries as being of great importance, and it was singled out for attention in several of his obituaries (e.g., Dunal, 1842; Brongniart, 1846). De Candolle's work initially stimulated a rather typological approach to floral organization in people like Michel Dunal, Christian Moquin-Tandon, and Auguste de Sainte-Hilaire. Since, however, the limits of plant groups remained vague, the typological approach did not flourish in systematics (Stevens, 1984b).

Linnaeus and Antecedents to the Cortex-Medulla Doctrine

Some of Linnaeus's predecessors had ideas that are—or might be—supposed to have had some influence on the cortex-medulla theory (see also Guédès, 1969). We discuss briefly some aspects of the work of Cesalpino, Mariotte, Grew, Malpighi, and Vaillant, so as to understand more clearly the background to Linnaeus's work.

Andrea Cesalpino, the noted Italian systematist, was considered by Linnaeus (1751a) to be the first, and one of the greatest, "true botanists" and was freely acknowledged (Linnaeus, 1738, 1749) to be the immediate source of the cortex-medulla theory. There is no detailed treatment of his work, although Greene (1983, and references therein) provided an entry into the literature. Cesalpino was a noted Aristotelian scholar, his book *Quaestionum Peripateticarum Libri V* (which we have not seen) being of importance in this context. Characters of the fructification, and particularly those of the seed, were most important in classification for Cesalpino because the multitude of parts they provided allowed distinctions between groups to be made (Cesalpino, 1583; see also Morton, 1981). But they were, of course, also very important functionally, being involved in that vital aspect of the plant's life, reproduction; they were vegetative substance allowing the plant to reproduce (Cesalpino, 1583).

The cortex-medulla distinction and the role of those two parts in the life of the plant pervade many of the introductory chapters of book 1 of Cesalpino's work, but as Sachs (1890) correctly observed, the relation between plant organs and these tissues is different from that usually described by Linnaeus (but cf. Linnaeus, 1747). Leaves in general were indeed produced from the cortex. Thus Cesalpino suggested that deciduous leaves were produced from the outer cortex, evergreen leaves from the inner cortex (liber: Cesalpino, 1583). The calyx and corolla, both on occasion called leaves (folium), were also of cortical origin, but the stamens (flocci) were not mentioned in this context. They were small, and their importance for reproduction was then unknown. It is in the discussion of the origins of the different parts of the fruit that the cortex-medulla distinction is most focused. The fruit arose from the inside of the plant and was made up of three tissues, medulla, lignum, and cortex, which in turn formed the seed and the woody ("cortex") and fleshy ("pericarp") parts of the fruit (*ibid.*, p. 18). The fruit developed after the flower, the stigma plus style ("stamen") of the former being the young fruit (*ibid.*, pp. 14, 19; see also Sachs, 1890).

The position of the medulla provided further evidence of its nature and significance, there being the overwhelming power of the analogy that Cesalpino (1583, p. 3; translated in Sachs, 1890, p. 46) drew at some length between the vital parts of animals and plants. Nature always concealed the principles of life ("vitalia principia") in the innermost parts, such as the viscera in animals. Hence in plants the principle ("principium") was to be found not within the cortex, but more internally—that is, in the internal medulla—of which much was in the stem but not in the root. The heart or soul of the plant, the "cor," was the junction of the root and the stem but extended throughout the plant. As Cesalpino (1583) noted, the leaves and fruits followed the nature of the cortex, the internal seeds that of the medulla.

Cesalpino's ideas on the parts of plants, their origins, development, and relationships need a more extended treatment than can be given here. However, it may be noted that catkins provided him with a challenge; he thought that in such structures flowers had changed into a different substance—more specifically, that the amentum was produced from the seat of the flower, with the "stamina" (pistils) forming the ament and the petals and sepals ("folia") and stamens degenerating into scales (Cesalpino, 1583; Sachs, 1890). Other flowers were also distinctive in the context of this discussion. Cesalpino surmised that in *Ornithogalum* and *Helleborus* the calyx and corolla were joined, since the leafy organs surrounding the flower were green on the outside and colored on the inside. The flowers of *Cucurbita* and *Punica* presented a different problem: here the calyx was continuous with the outer cortex of the fruit, the flower originating from the fruit ("flos in radice fructus exoritus"—Cesalpino, 1583, p. 16; Greene, 1983, p. 820). Cesalpino also noted the rarity of plants in which flowers were borne directly on branches with thick bark and the progressive purification of the sap of the plant in the flower.

In none of the other works mentioned below (or in Guédès, 1969) does the cortex-medulla distinction assume such prominence. Nehemiah Grew (collected in his *Anatomy of Plants,* 1682; see also Arber, 1941, and Morton, 1981) indeed noted that there were only two parts of the plant that were fundamentally ("essentially") distinct: the pithy part and the ligneous part, "or such others as are analogous to either of these" (Grew, 1682, "Philosophical History," p. 19). However, in his discussion of the anatomy of different plant organs, including seed and fruit, Grew emphasized not "pith" and "wood" but the particular nature of the tissues making up these parts. Although the several tissues of the plant were compounds of these two parts (Grew, 1682, "Anatomy") there were other interesting levels of analysis.

However, the pith was very important because sap moved through it in large part, and the energy and nutritive quality of the sap determined the particular part of the plant that developed; in general, there was progressive purification of the sap as it moved through the plant (Grew, 1682, "Anatomy"). The flower promoted the ascent of the sap, so if there was no flower, the fruit would die. If the flowers were large, much sap would be present, but it would be used up by the flower "like a greedy Nurse, that prepares the Meat for her Child, and then eats it up herself" (Grew, 1682, "Anatomy," p. 37). The intrinsic rate of ascent of the sap of a species was also important; grapes, with rapidly ascending sap, had almost no flower since no increase in sap that the flower could provide was needed.

This is not so different from either the physiological-balance theory of development that Linnaeus propounded, or the ideas put forward by Edme Mariotte

(1679), although Sachs (1890) attributed to Mariotte in particular Linnaeus's idea that the medulla grows by extending itself and its envelopes in a form of intussusception; the pressure of the sap makes the parts of the plant expand. Mariotte (1679, pp. 54, 55) noted that in cuttings the pith ("mouelle") imbibes water like a sponge "and transmits it in the little fibers between the bark and the wood, from where it is pushed in part towards the end of the base to produce roots at the extremity of the little point, . . . and in part to the nodes which are in the air, to make the buds there swell up, and to make them extend in branches and leaves." In his extended analogy between plant and animal nutrition, Mariotte conceived of the former as progressive purification of the sap after initial "digestion" by the root.

Guédès (1969) discussed at length the several indications Grew gave that he recognized an equivalence among cotyledons, leaves, and even calyx and corolla. Such equivalence was widely noted. Marcello Malpighi (1686), who with Grew is considered to be a founder of plant anatomy, discussed such transitions extensively (see also Mobius, 1901; Arber, 1941; Guédès, 1969). Sebastian Vaillant, in his important *Sermo de Structura Florum* (1718) (see Stearn, 1957; Larson, 1971; Stafleu, 1971) dealt largely with sexual reproduction in plants. However, when discussing the transition of stamens and carpels into petals in doubled flowers, he adopted a style of explanation very similar to Grew's (see also Guédès, 1969).

Enough has been said to discern the relationship between Linnaeus and earlier authors in the context of the cortex-medulla theory. The general outline of this theory as found in Linnaeus is evident in Cesalpino (1583), although some details differ substantially. Cesalpino's emphasis was on the fruit and seed, the functions of the flower being poorly understood in his time (see Greene, 1983). Linnaeus, stimulated especially by the discovery of the sexual functions of the different parts of the flower, focused more on the flower. Cesalpino emphasized the importance of the internal structure of the organism as the place where the principles of life resided, hence Linnaeus's (1738) early suggestion that the flower represented the insides of the plant exposed by the tearing of the cortex. By and large, similar flowers presented problems to both Cesalpino and Linnaeus—*Ornithogalum* and catkin-bearing plants figure prominently in the work of both. Embryonic ideas of the transformation, metamorphosis, or general equivalence of plant parts were widespread, being evident in the works of Grew, Malpighi, Vaillant, and other authors (see Arber, 1946; Guédès, 1969).

The expansive power of the sap is alluded to in Mariotte's work, while the constrictive effect of thick outer cortex on the development of flowers and fruits was suggested by Cesalpino. The general idea of plant nutrition in the seventeenth and early eighteenth centuries, exemplified in the work of Mariotte and Grew in particular, is that of progressive purification of the sap coming from the roots, but there was known to be movement of fluid in the other direction as well. The development of particular plant structures was generally considered to be dependent on the presence of the right kind or amount of sap.

Cesalpino himself developed the cortex-medulla theory from a rather tentative analyses of the plant advanced by Theophrastus (for details, see also Greene, 1983). Theophrastus distinguished between core and bark, with wood occupying a somewhat ambivalent position—perhaps a part of the bark or a tissue coordinate with it. This is the third level of organization; these tissues are in turn made up of varying amounts of flesh, fibers, and sap, while moisture and warmth are the fundamental properties of the plant body (the formal structure of Grew's idea of the plant is similar to this). The composition of plant organs is discussed (Theophrastus, 1916) in terms of the tissues making up the second level of organization. In line with arguments later advanced by Linnaeus and others, Theophrastus (1976) noted that the distribution of food in the tree affected fruiting, excessive food to the vegetative growth being prejudicial to the fruit and leading to a failure to bear.

DISCUSSION

Linnaeus's classically inspired idea that in the flower the inner structure of the plant, its *real* structure, becomes evident to the human eye is central to an understanding of his botanical thought in particular, but to much else besides. The medulla, the form-generating part of the plant, entered most completely into the formation of the pistil and seed and was surrounded by structures representing the different parts of the cortex. The cortex, especially in its vegetative aspect, was largely disposable from the point of view of the adult plant, and this, when joined with his views on plant sexuality, justified the emphasis on the characters of the fructification in the formation of natural genera (e.g., Linnaeus, 1751a). The cortex-medulla theory is also intimately involved in the notion of both prolepsis and metamorphosis, and to a considerable extent in the broad outlines of his arrangement and understanding of living beings, especially of plants and "plantlike" animals.

Clearly, Linnaeus's development of this idea in plants was also influenced by discoveries about *Hydra, Volvox,* the "individuality" of each segment of the tapeworm, and so on, as extensively detailed by Broberg (1985), but Broberg's thesis (p. 167) that "zoology rather than botany steered Linné's mental activity" is perhaps a little overstated. To him (p. 162), "The reproduction observed for the polyp had to affect the conception of reproduction in the main, and it is necessary to consider Linné's very personal marrow-bark [medulla-cortex] doctrine in light of what the polyp-tapeworm had enlightened him about; less so as a result of his botany." In a somewhat similar vein, Larson (1971, p. 106) noted that "Linné had taken note of this theory [the cortex-medulla theory] as early as 1738, but he only found a use for it fifteen years later" in his ideas about hybridization. In the thesis *Taenia* (Linnaeus, 1748) the animal body is indeed discussed in much the same style, although with a terminology rather different from that Linnaeus adopted very soon afterward for plants. However, the cortex-medulla theory is evident in his earliest work. The classical flower became integrated into a new, all-encompassing vision, but the general background to this was accessible to even the young Linnaeus. The assertion that there was a fundamental similarity among all the appendicular parts of the plant, whether via metamorphosis or anticipation, is the culmination of this vision.

In particular, the theory of prolepsis, or anticipation, seems itself not to have been anticipated in any detail in earlier literature. Linnaeus considered his ideas on prolepsis to be very important (he wrote concerning prolepsis in one of his autobiographical fragments, "Nobody has penetrated further into the secrets of the creation" (Pulteney, 1805, p. 558)); the mysteries of Nature were revealing themselves to him. Linnaeus (1760c, pp. 1, 2; see also Linnaeus, 1763) strongly asserted that his ideas were new:

> Nobody will readily have doubted that the nature of the plant is much simpler than that of animals to such a degree that it is not surprising if in the latter it is difficult to penetrate into the inner recesses of the science. Malpighi and Grew themselves attempted to prepare the way using anatomy, Hales and others by physiology. In truth I have advanced by a third way proposed by me, the lead to be followed in section 10, p. 826, in the Systema Naturae [ed. 10, 1759b, in part translated above], so that others who are unaccustomed to it can follow it without a mistake.

This is by way of introduction to the thesis *Prolepsis Plantarum,* in which he developed the parallel between the growth of the flower and that of the vegetative shoot. Of course, Linnaeus was in general not one to hide his light under a bushel; he also thought that his fragments of a natural method were a masterpiece, and that much else he had done was of similar importance (Malmeström & Uggla, 1957; Larson, 1971; Lindroth, 1983).

Here, perhaps, is a clarification of his apparently hasty dismissal of anatomists as mere likers of botany—botanophiles--whose work did not pertain to the science of botany (Linnaeus, 1736b, 1751a). Stephen Hales, Johann Gesner, and Christian Theophilus Ludwig, all interested in the "laws" of botany, the anatomists Grew and Malpighi, and the physiologist Bernhard Feldman were all included in this sorry group. Their discoveries, whether in anatomy or physiology, did not pertain to an understanding of that aspect of plants by which their essence was revealed and their form in general made manifest. Those physiologists who were included among the "philosophers" of botany—Thomas Millington, Joachim Camerarius, Vaillant, and Johann Gustav Wahlbom—were mentioned because their work contributed to an understanding of plant sexuality. This was of much more central importance to Linnaeus's thought than findings on cell structure, and he credited Millington and colleagues with having revealed the laws of nature and the mystery of sex. Earlier, Linnaeus (e.g., 1741) had characterized the work of the botanophiles by its lack of interest in the fundamentals of botany; that is, it was not involved in the disposition of plants (into species, genera, orders, classes), or in their naming.

It may also be noted that Linnaeus (1751a) observed, albeit with some reluctance, that the use of a lens was not essential to an understanding of his sexual system, despite some people's protestations. Microscopes were, however, essential in anatomical work, even if an anatomist like Grew deliberately started out by recording what the unaided eye could see, only after that using a lens. Interestingly, Linnaeus seems to have been dissuaded by Albinus (probably Bernard Sigefred Albinus; see Mirbel, 1810) from following up on an initial wish to study anatomy. Anatomy and taxonomy did not begin to be integrated in botany until the late nineteenth century.

The ideas of prolepsis and metamorphosis in particular allowed Linnaeus to account for much variation that was not relevant to his classification but that nevertheless existed and so could not be entirely dismissed. This point is a very important one. As Guédès (1969) correctly observed, in this new way of looking at a plant, Linnaeus paid close attention to teratological phenomena and similar variation that he necessarily ignored when working on the limits of genera in the sexual system. Examples of the term "varietas" included double and proliferous flowers and other trivial variation of no taxonomic importance (Linnaeus, 1744). Luxuriant flowers, including both the double and proliferous flowers mentioned above, were always monstrous, never natural (Linnaeus, 1751a). All double flowers were at most varieties, and variety never could be the basis of real species (Linnaeus, 1762b). This was reasonable from Linnaeus's taxonomic viewpoint. The essences of species never changed, so how could these variants, the expression of which often depended on the fertility of the ground in which they were grown, represent that essence? (However, see Ramsbottom, 1939.) In Linnaeus's morphological work they could, however, be evidence of the potentiality of plant form. In this alternative way of understanding plants, what is accidental variation in one situation becomes important evidence of the real nature of structure in another.

As with Goethe, there is no clear idea of a type[14] or ideal plant in Linnaeus's morphological writings; there is simply a continuum of form. Although at first sight all appendicular organs are best interpreted as modified leaves (this is a reading of some passages in Linnaeus—e.g., 1760c, p. 19), this would seem to run counter to Linnaeus's statements that the anthers, stigmas, and seeds were the essential parts of the flower: how could structures essential at high levels of classification be modified from those essential only at low levels? However, since Linnaeus noted that the medulla was involved in the production of all appendicular organs, the leaf or calyx could be considered simply as two parts of the "shoot" from the cortex modified by the medulla; the taxonomically most important structures were those closest to the maternal forces in the medulla.

Thus the form-making potentiality of the plant largely or entirely resided in the cortex, although for its expression in visible form involvement of the cortex with the medulla was essential. That the pistil (largely pure medulla) changed its form in some terata is not to be interpreted as a demonstration of the interchangeability of medulla and cortex (cf. Guédès, 1969) but simply as the medulla failing to penetrate the cortex or penetrating it more strongly than was usual in a flower (a discussion on staminate flowers is along the same lines—Linnaeus, 1763). The medulla stimulated the production of organs appropriate to the balance of physiological forces in the plant, only in the pistil perhaps in part determining form. Otherwise the medulla itself was largely formless; even in the flower it could be argued that carpels took different forms, especially in terata, because they had a thin cortical covering, although Linnaeus does not seem to have gone that far.[15] However, his explanation of the malleability of

[14]As Brady (1987) and some others (e.g., Lenoir, 1987) have rightly emphasized, there is also no notion in Goethe's early botanical work of a definite form that is the "type" of all appendicular structures and to which all others must ultimately be reducible; all appendicular organs are not modified leaves, or modified anything else for that matter (see also Arber, 1946).

[15]Guédès (1969) thought that Linnaeus's flower was polyaxial, but this seems too "modern" an interpretation. As we saw, Linnaeus did not distinguish clearly between axillary and terminal buds.

form in species of *Chaos* and his theory of hybridization, in which God created a single medulla that became differentiated only by contact with a series of different cortices during successive hybridizations, confirm that pure medulla lacked particular form.

Hence Linnaeus had achieved a fairly comprehensive explanation of the material cause of form. The substance of the organism (cortex) was dissociated from the essence (medulla) that generated the form that substance assumed, and essence became manifest in substance. The efficient cause of plant form is the physiological-balance theory described above. But hybridization and continuity compromise any attempt to make simplistic explanations of the later Linnaeus as being a rigid typologist.

One strand of thought in pure morphology is an emphasis on the continuity of form, as illustrated by the comparison of different organs showing intermediate structures more or less out of any context supplied by the taxonomic relationships of the organisms bearing those organs (see Stevens, 1984c). It is this kind of continuity that is evident in Linnaeus's morphological writings. The "plenitudo" that he emphasized (Linnaeus, 1755a, p. 7) is both a simple fullness or doubling of a flower and also a phenomenon that leads to the confirmation that there is continuity or plenitude in the world of pure form. Morphological plenitude in particular interrelated a number of diverse phenomena in the world of plant form; unruly form was at least reduced to order, even if not completely understood. Indeed, the "Linnaean" cortex-medulla theory of plant tissues and the physiological-balance theory of the vegetative-floral distinction provided him with a rather full and complex understanding of form. His work on what we would call pure morphology concentrated more on nature's similarities than on its differences and led him to an apparently satisfying and truly systematic comprehension of the plant world.

But Linnaeus was also the quintessential classifier and namer, and here he proceeded in a largely analytical fashion. Yet despite these extensive and time-consuming classificatory studies on which he dealt with the flood of novelties pouring into Uppsala from correspondents around the globe, he attempted the partial synthesis of a world of systematically grouped form as a continuum, at least at the suprageneric level (e.g., Linnaeus, 1737, 1751a; Linnaeus's correspondence with Albrecht von Haller--see Smith, 1821, Vol. 2; Daudin, 1926).[16] As already noted, hybridization—in which the cortex-medulla theory played an important, if poorly understood, role—could generate this continuity. It explained the arrays of similar species being discovered in genera like *Geranium* and *Erica* and the lack of distinction between genera assembled into natural groups (Linnaeus, 1744 (see Ramsbottom, 1939), 1762b). At a yet higher taxonomic level, the cortex-medulla theory and prolepsis together enabled Linnaeus to demonstrate that a number of animals were like plants in important respects, and so continuity was evident there as well (see TABLE 2). New discoveries in

[16]Since many plants remained to be discovered, Linnaeus had a ready explanation for apparent gaps. Such gaps are clear in the diagram of relationships of Linnaeus's *ordines naturales* (families), believed to be based on one drawn by Linnaeus himself (Giseke, 1792). Some families touch, but most are separated by gaps of varying sizes.

the microscopic world hardly disturbed the link between *Hydra,* with its sensitive flowers, and the other Zoophyta, with flowering plants. *Volvox chaos* was well positioned. The dissolution of form it seemed to suggest in its terminal position in the animal kingdom was not the change from animals to plants, which was a gradual change rather than dissolution anyway, but the loss of form that heralded the discovery of a new kingdom. In its formlessness, capacity for increase, and activity was evidence of the very principles of life, life in its purest and certainly simplest form—pure medulla (see also Broberg, 1985).

The cortex-medulla theory or, more generally, Linnaeus's ideas on the construction of organisms also helped his understanding of how and why organisms could live together in the world (i.e., order between organisms in the living world; it was used to explain a yet higher level of causality) (see, for example, Lindroth, 1983). Many of the properties of plants, including their palatability to insects and, perhaps not surprisingly, their medicinal attributes (Linnaeus, e.g., 1747, 1752; Giseke, 1792),[17] are constant in genera and higher groups in a natural classification. Such properties reside in the medulla, which is at the same time at the heart of natural classifications in general. The close association between plants and insects was evident in that some insects tended to eat plants of different species of the same genus (Linnaeus, 1752; 1760a); perhaps insect larvae could teach us about the medicinal properties of plants (Linnaeus, 1749; see also Linnaeus, 1751b). This close, although rather one-sided, association was strengthened for Linnaeus because the larvae of both groups metamorphosed to produce the adult, hence the listing of both insects and plants in the thesis *Pandora et Flora Rybyensis* (Linnaeus, 1771). Such an interlocking of ideas would allow Linnaeus at least partially to sidestep the issue of whether God had created a definite number of species; even if he had not, hybridization might not increase the number of different ecological or functional units in nature. Commenting on the later Linnaeus, Broberg (1985, p. 180) remarked: "What he needed was a principle which gave causality to creation, not blind faith." That principle was largely based on the cortex-medulla theory.

Linnaeus's world of systematic continuity was different in nature from that of morphological continuity. Although both are to an extent based on the cortex-medulla theory, the latter more directly than the former, they use different observations to support the different constructions of continuity. Linnaeus would surely have approved of the comment that P. J. F. Turpin (1815, p. 429) made when discussing possible interrelationship of inflorescence types: "But why have we need to make abstractions, since nature never fails to show herself all the intergradations which can illuminate us?" (Early in his life in particular, Turpin was strongly influenced by Goethe.) There is little evidence of discord between the two kinds of continuity in Linnaeus's own work; both stemmed from his observations of nature. As a further complication, genera

[17]The opposition between the masculine, external, vital cortex and the feminine, internal, animal medulla is the key to Linnaeus's concept of medicine. Since it also involves an opposition between taste and smell and a hefty dose of numeralogy (the number 5 again), Linnaean medicine is less than easy to understand (Linnaeus, 1766b; see also Hjelt, 1907; Lindroth, 1983).

and higher taxa that in the taxonomic scheme of things needed to be separated by distinctive and constant features were associated in an arrangement of a kind that allowed the reader to develop ideas of continuity and even change—as also in Charles Bonnet and J. B. A. P. M. de Lamarck (see Lovejoy, 1936—he barely mentioned Linnaeus). Further, prolepsis, metamorphosis, and hybridization are more directly subversive of a world of discrete, separate entities. The tension is however, evident to us, the tension between nature dynamic and flexible and nature ordered rationally, preferably with gaps.

Historically, however, there has all too often been overt or covert conflict between systematists and evolutionists (the work of the latter is dependent for a considerable part on the systematic patterns produced by the former) and proponents of pure morphology (see, for example, Cusset, 1982; Wetzels, 1985; Appel, 1987; Brady, 1987; Portmann, 1987). Wetzels (1985, p. 145) wrote eloquently about Goethe's approach: "It is this delicate simultaneity of the concrete immediacy of individual observation and the equally concrete presence of a picture of a whole, that Goethe had described earlier as 'tender empiricism,' an empiricism which was capable of making the individual phenomenon transparent so that the whole of which it was not so much a part, but a manifestation, became visible." But of course words such as "empiricism" and the like have different meanings for proponents of these two approaches; there are tensions between the phenomenological Goethean and the somewhat-more-circumscribed Linnaean approaches to morphology (see above) and more conventional systematics and science (see Amrine & Zucker, 1987; Sattler, 1986). The form of the organism may not have the same meaning or significance for the proponents of the two approaches. Lindroth's (1983) important essay almost casually captures this dilemma. He emphasized that Linnaeus was preeminently an empiricist, an acute and enthusiastic observer, a voluptuary of nature, and an empirical genius, yet somebody who made no major contributions to science. In his systematic work empiricism was subservient to an overwhelming desire for order. Yet in the cortex-medulla theory an almost "tender empiricism" combines with order because the theory explains why and how the world is as it is. As a theory, it proved to be of little interest even to his contemporaries. Linnaeus's way of establishing order, as Lindroth so clearly demonstrated, was hasty, superficial, and to a high degree inductive, as well as being based on a questionable philosophy of life.

The conflict is less evident in Goethe's work. As is well known, he had earlier found the Linnaean system, and the terms associated with it, intellectually unsatisfying. Goethe disliked counting and analyzing, which he thought that Nature abhorred, but these were needed if he was to use the Linnaean system. Goethe also observed how the same organ varied in shape on a single plant, and to him this suggested problems with terminological categorization (see, e.g., Arber, 1946; Guédès, 1969; Wetzels, 1985). Of course, the Linnaean sexual system was not the most natural arrangement when it came to the delimitation of larger groupings of plants (cf. Stafleu, 1971), although a few groups, such as the Gynandria-Diandra, the Didelphia-Decandra, and the Tetradynamia-Siliculosa were more or less composed of related genera (Orchidaceae, Leguminosae, and Cruciferae, respectively; see Linnaeus, 1753). Thus, neither the terms

Linnaeus used for plant parts nor Linnaeus's sexual system itself led Goethe to a satisfactory understanding of plant form or diversity. However, his ideas on metamorphosis did just this, albeit in a largely asystematic context.

Goethe and Linnaeus drew the data they synthesized into their respective visions of continuity—metamorphosis, prolepsis, a modified *scala naturae*—from their appreciation of the world of external form. Belief in the continuity of organic form persisted in the systematic community well into the nineteenth century; it was believed, echoing Linnaeus, that if there were gaps in the system of nature, they would eventually be filled. But the similarities go further. Linnaeus's valuation of anatomy resonates with the work of A.-L. de Jussieu, a founder of the new "natural method" in systematics. For De Jussieu (1778) the functions of the relatively few plant structures that were used in classification were known; those structures were almost all external, and there was no need to study their anatomy. Of course, his remarks were made in a systematic context, and those of Linnaeus some 20 years before in a largely morphological context, yet both men emphasized the external appearance of the plant as being a suitable object for study, and the two produced natural arrangements that are similar in their basic principles. The world of external form may turn out to be an unreliable guide to both systematics and anatomy, and continuity in one guise or another, or at least reticulating relationships, are the likely results of an analysis of external form. De Jussieu's natural method is as explicitly based on assumptions of continuity as Linnaeus's conception of life, and his *Genera Plantarum* (De Jussieu, 1789) can be analyzed in the same way as Linnaeus's Vermes, and with similar results.

Linnaeus, with a view of life notably archaic or anachronistic even for its time (see, for example, Cain, 1958; Stafleu, 1971; Lindroth, 1983; Hull, 1985), embraced the Aristotelian notion of plenitude and worked it out in the context of a natural arrangement of groups, the characters of which were all to be discerned by the naked eye. The hylomorphic cortex-medulla theory aids in our understanding of this natural arrangement. It provides features that serve to bind the larger units of the arrangement into an indivisible, albeit branching, continuum rather than to separate them, in the process showing clearly that the units are not discrete. It also justified the selection of characters used in classification. In a similar fashion, Linnaeus developed an approach to the analysis of plant form that embraced another manifestation of plenitude, the fundamental similarity and interconvertibility of the appendicular organs of the plant. The rather archaic basis of this thought should not blind us to its evident power in synthesizing a very disparate body of observations.

It is noteworthy that the cortex-medulla theory is best developed in plants and fungi. For plants, Linnaeus based his ideas on his own observations of exterior form and on Cesalpino's seventeenth-century theory, largely ignoring the work of Grew and Malpighi; for fungi, his thoughts were sparked by Münchhausen's disputed findings. In animals, the theory is most evident in Linnaeus's discussion of the least-understood and smallest organisms, albeit those on which some of the most exciting discoveries of the day were being made. It was most successful where knowledge was least well established, serving to guide him through these areas of uncertainty; the theory colored both his observation and his interpretation of other people's data (see Le Guyader, 1988). As with the "*nemesis divina,*" "reality must—once again—adjust itself to the scheme" (Lindroth, 1983, p. 53).

Linnaeus's theory was epitomized in the name changes of that almost animal, almost plant, almost a member of a new kingdom: *Volvox chaos* became *Chaos proteus. Chaos* itself was a genus of half-misinterpreted observation at the limits of one particular man's late-eighteenth-century vision. The fate of Linnaeus's theory was like that of *Furia,* a new genus described by Linnaeus and placed adjacent to *Chaos* in the twelfth edition of the *Systema Naturae* (see Lindroth, 1983). The sole species in the genus, *Furia infernalis,* was Linnaeus's contribution to the book of imaginary beings; it never existed, despite the fact that a vicar, no less, reported that one had fallen onto his plate. The vicar and Linnaeus alike were mistaken, and as we saw above, De Candolle rejected the cortex-medulla theory because monocotyledonous plants simply did not have pith. Similarly, J. G. Kölreuter's experiments on hybridization (see Roberts, 1929; Mayr, 1986) showed that crosses in which the same species was first the female parent, and then the male parent, tended to produce the same kind of hybrid: there was no maternal dominance; there was not even any hybridization. Even so, ideas of metamorphosis in particular and change in general are so pervasive in Linnaeus's later works that their influence should not be entirely discounted.

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